

**A LIFE HISTORY APPROACH TO THE STUDY OF PLANT SPECIES RARITY:
Gentianopsis crinita IN NEW YORK STATE**

**A Dissertation
Presented to the Faculty of the Graduate School
of Cornell University
in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy**

**by
Heather Jane Robertson
August 1992**

© Heather Jane Robertson 1992
ALL RIGHTS RESERVED

Author's note: The content of this digital version of my thesis is the same as the original paper version but the text has been re-formatted to reduce the size of the document and, as a consequence, the thesis has been re-paginated.

A LIFE HISTORY APPROACH TO THE STUDY OF PLANT SPECIES RARITY:
Gentianopsis crinita IN NEW YORK STATE

Heather Jane Robertson, Ph.D.
Cornell University, 1992

Gentianopsis crinita (Froel.) Ma, (fringed gentian), is a rare biennial plant, native to eastern North America. Generalizations about the life history characteristics of biennials, and the habitats where these plants occur, provided a framework for examining the critical factors affecting the rarity of *Gentianopsis crinita* in New York State. The relative significance of these factors was assessed by comparing *Gentianopsis crinita*'s responses to those of *Daucus carota* L. (wild carrot), a common biennial that occurs in the same localities as *Gentianopsis crinita*. The principal study sites were two old fields near Ithaca in Tompkins County, and a landslide at Letchworth State Park in Livingston County.

In one old field, seeds were sown in experimental treatments that represented successional habitats ranging from bare ground to scrub more than 3 m tall. Survival and reproduction of both species were enhanced where interspecific competition was reduced by ground disturbance and clipping of vegetation, but both species also persisted among tall herbs and low woody shrubs less than 1 m high. Neither species survived in tall scrub. Experiments indicated that *Gentianopsis crinita* may lack a persistent buried seed bank, and according to previous studies, so does *Daucus carota*. Flowering individuals of *Gentianopsis crinita* had a higher seed output on average than *Daucus carota* despite greater losses to herbivores.

Although *Gentianopsis crinita* performed at least as well as *Daucus carota* in all these ways, observations and experiments revealed that the distribution and abundance of *Gentianopsis crinita* were more limited by its narrower tolerance of edaphic conditions. In contrast to *Daucus carota*, survival and growth required relatively high soil moisture levels and circumneutral to alkaline soils. The results also demonstrated that the optimal ecological conditions for *Gentianopsis crinita*, where survival, growth and reproductive output are greatest, can shift spatially over time, because patches of more fertile soils sometimes have inadequate moisture.

Recommended conservation action includes permanent prevention of scrub encroachment on preserves and the selection of preserves containing refuge areas that are wet enough to maintain populations even in dry years.

BIOGRAPHICAL SKETCH

Heather Robertson spent her childhood travelling abroad and in Britain with her parents, who were in the British Army. She lived in Singapore and Aden and was lucky enough to visit the National Parks of Kenya. She graduated from Durham University, England in 1974 with a First Class Honours degree in Botany and Geography. She pursued her developing interest in ecology and conservation by completing a M.Sc. degree in Conservation, with Distinction, at University College London in 1977. After graduating, she lived in the English Lake District for over 8 years and obtained practical experience in nature conservation by working as the Ecologist for the Lake District National Park and as an Assistant Regional Officer for the Nature Conservancy Council, the British government's advisory agency. In 1985 she was given leave by the Nature Conservancy Council to study for a Ph.D. in plant ecology at Cornell University, to increase her scientific expertise. In 1990 she returned to the Nature Conservancy Council in England and joined its team of national specialists in the Science Directorate as a grassland ecologist.

To
Catharine,
Joy
and
Deborah

ACKNOWLEDGEMENTS

My thanks go to my committee members, Dr. Robert Cook, Dr. Peter Marks, and Dr. Charlie Smith, for all their help during my time as a graduate student. Bob Cook not only gave me the chance to carry out research in plant ecology, but also, in his role as Director of Cornell Plantations, enabled me to gain direct experience of nature conservation in the United States. I greatly valued this opportunity to be involved in the Plantations' important work of conserving the University's Natural Areas.

Two ecologists whose research I found particularly inspiring during my project deserve special mention: Dr. Peter Grubb of Cambridge University, United Kingdom, and the late Dr. Deborah Rabinowitz. Deborah was a member of my committee, but unfortunately I knew her for only for a brief period before her untimely death in 1987.

Staff at Cornell Plantations and the members of the University's Natural Areas Committee were all extremely helpful about my thesis project, and I hope that my work will in turn assist them in their efforts to conserve the fringed gentian. Dr. Nancy Ostman, Hal Martin, Dr. William Hamilton, Jr., Dr. William Dress and Robert Dirig gave freely of their time and experience. F. Robert Wesley not only provided information on past and present gentian localities but was also endlessly patient in helping me to identify American plants.

Douglas Bassett, the Naturalist at Letchworth State Park, gave me a great deal of valuable information and assistance. Other naturalists also made very useful contributions to my project including Greenleaf Chase, Bonnie Glickman, Dorothy McIlroy, Mary Kelsey, Bente King, Dr. Pat Martin, Ron Pappert, Kenneth Paul and Edith Schroott. Permission to visit various gentian sites in New York State was kindly given by the landowners, including Mr. and Mrs. Robert B. Jones, the Kelly family, Robert Otter, the Bergen Swamp Preservation Society and the Burroughs-Audubon Nature Club. State Heritage Program staff across the northeastern United States and the government conservation staff in Canada provided much useful information on the status and distribution of the fringed gentian.

Many of Cornell's faculty, research associates and staff gave me help and guidance. In particular I thank Dr. Karl Niklas, for investigating seed dispersal of the fringed gentian with me, Dr. Susan Riha, Dr. David Bouldin, Dr. Ray Bryant and his assistant Emmy Lucas for their help with soil analyses, Dr. Keith Eggleston for climate information, Dr. John Franclemont for identifying insects, Dr. Tom Weiler for advice about growing gentians in the greenhouse, Dr. David Winkler for discussions about life history models and dispersal experiments, and Dr. Chuck McCulloch, Dr. Hugh Gauch and Dr. Philip Dixon for advice on statistics. People from other organizations who gave me advice and assistance included Dr. Hugh Iltis from the University of Wisconsin, Dr. Norton Miller of the State Museum of New York, Dr. Ferguson of the USDA's Systematic Entomology Lab, Dr. Klaus Satler of the British Museum of Natural History and Dr. Robert Young of SUNY Geneseo.

Essential funding was provided by an International Fellowship from the American Association of University Women, a fellowship given to me by the Josephine De Karman Trust, grants from the Cornell and national chapters of Sigma Xi and from the Rabinowitz Graduate Student Research Fund and the Robert H. Whittaker Memorial Fund.

I am very grateful to the Nature Conservancy Council of Britain, for giving me special leave to undertake my Ph.D. degree at Cornell, and to staff from NCC's successor body, English Nature (NCC England), for all their support, in particular Dr. Keith Kirby, Dr. Rick Keymer and Dr. John Hopkins.

Special thanks go to my fellow graduate students at Cornell, for their willingness to discuss ideas and for their immediate response when I needed volunteer labor! Steve Anderson, Sana Gardescu, Laura Jackson, Felix Sperling, Mark Witmer, and research associates Dr. Aaron Ellison and Dr. Robert

Muller combined their efforts to make an extremely effective "bulldozer," which cleared scrub from the Fringed Gentian Natural Area in a matter of minutes. John Andersland, Curtis Bohlen, Cynthia Jensen, Beate Nürnberger, John Saponara and Sara Tjøssem were among other grad students who gave me ready assistance during my project. Between 1988 and 1990 I was also lucky to have three cheerful and enthusiastic research assistants, Jim Murray, Carolyn Tomaino and Laurie Isenberg. Family and friends helped me along too, especially Debbie Joseph, who managed the transition from librarian to plant ecologist with ease. Among all the many people who contributed to my project, I owe my greatest debt of thanks to Sana Gardescu. She helped me in innumerable ways throughout my time at Cornell and held together the American side of my thesis production when I returned to England. I simply could not have completed my thesis without her constant and unstinting encouragement and support.

TABLE OF CONTENTS

Chapter 1	
INTRODUCTION	14
Chapter 2	
BIOLOGY OF <i>Gentianopsis crinita</i> AND DESCRIPTIONS OF THE STUDY SITES	20
INTRODUCTION	20
BIOLOGY OF <i>Gentianopsis crinita</i> (Froel.) Ma	21
Taxonomy	21
Historical background	21
Distribution, abundance and conservation status of <i>G. crinita</i>	22
Life cycle and morphology of <i>G. crinita</i>	26
Floral biology	28
Senescence and the effect of frost	29
BIOLOGY OF <i>Daucus carota</i>	29
THE STUDY SITES	32
Description of the Ithaca study sites	32
The Radio Lab site	32
The Natural Area	33
Description of the Letchworth study site	34
Climate and weather of the study sites	35
Chapter 3	
PERSISTENCE, REGENERATION AND COLONIZATION BY <i>Gentianopsis crinita</i> IN A CHANGING LANDSCAPE	38
INTRODUCTION	38
SECTION I. PERSISTENCE OF <i>G. crinita</i> IN SUCCESSIONAL HABITATS	39
Introduction	39
Materials and Methods	40
Experiment in the existing clearings: 1987-89	40
Experiment in the scrub: 1987-89	43
Environmental measures and herbivory	44
Data analysis	45
Results	46
Experiment in the existing clearings	46
Experiment in the scrub	52
Comparison of species performance, environment and herbivory between the clearings and tall scrub	53
Discussion	59
Seedling emergence	61
Size, survival and flowering	62
Environmental and biotic factors	63

CHAPTER 3 (continued)

SECTION II. REGENERATION IN SITES WITH EXISTING POPULATIONS OF <i>Gentianopsis crinita</i>	64
Introduction	64
Materials and Methods	65
Experimental layout	65
Data analysis	66
Results	66
Area of microhabitats	66
Seedling emergence	66
Seedling survival	69
Discussion	72
SECTION III. COLONIZING ABILITY OF <i>Gentianopsis crinita</i> IN RELATION TO SEED DISPERSAL IN TIME AND SPACE	73
Introduction	73
Dispersal in time: the seed bank of <i>G. crinita</i>	74
Introduction	74
Buried seed bank: two experiments in the Natural Area	75
Rate of decline in seedling emergence over time:	
field experiments	75
Length of seed dormancy: four greenhouse experiments	76
Dispersal in space	77
Introduction	77
Wind dispersal	77
Dispersal by water	81
Animal dispersal	82
Discussion	82
Dispersal in time	82
Dispersal in space	84
Chapter 4	
REPRODUCTIVE PERFORMANCE OF <i>Gentianopsis crinita</i>	86
INTRODUCTION	86
METHODS	86
Production and loss of flowers, fruits and seed capsules	86
Seed dispersal	87
Estimation of relative reproductive output	87
Seed numbers and weights	87
Timing of reproductive events	88
Data analysis	88
RESULTS	88
Production and loss of flowers, fruits and seed capsules	88
Effect of loss of stem-tops on <i>G. crinita</i> 's flower production	93
Seed dispersal	94
Seed numbers and weights	97
Timing of reproductive events	99

CHAPTER 4 (continued)	
DISCUSSION	99
Seed numbers	99
Seed mass	101
Causes of losses to reproductive output and implications for conservation management	102
Chapter 5	
THE SPATIAL DISTRIBUTION AND RELATIVE RARITY OF <i>Gentianopsis crinita</i> IN THE LANDSCAPE	104
INTRODUCTION	104
SECTION I. SITE SURVEY	105
Materials and methods	105
Data analysis	108
Soil moisture indices	108
Results	109
Habitat types and associated species	109
Elevation, slope and aspect	110
Cover types	112
Soil types	114
Population size	116
Relative abundance: Density of plants	116
Reproductive performance	119
Summary of Section I	121
SECTION II. PATTERNS OF DISTRIBUTION, ABUNDANCE AND SURVIVAL OF <i>G. crinita</i> WITHIN A SITE	121
Preliminary studies	122
Transect study	128
Materials and methods	128
Data analysis	128
Results	129
Seed transplant experiment	137
Methods	137
Results	137
Transplants of <i>G. crinita</i> in pots	138
Methods	138
Results	139
Summary of Section II	141
SECTION III. GREENHOUSE EXPERIMENTS TO TEST THE EFFECT OF SOIL TYPE AND SOIL MOISTURE ON SEEDLING EMERGENCE, SURVIVAL, AND SIZE OF <i>Gentianopsis crinita</i>	141
Preliminary studies	141
Greenhouse experiment with 3 soil types	142
Methods	142
Results	142

CHAPTER 5, SECTION III (*continued*)

Greenhouse experiment with 5 moisture treatments	146
Methods	146
Results	148
Greenhouse experiment: moist vs. waterlogged conditions	151
Methods	151
Results	151
Summary of Section III	151
DISCUSSION	152
Factors limiting populations of <i>G. crinita</i>	155
Edaphic factors	155
Competition	157
Herbivory	158
Interactions among factors	158
Habitat specialization, physiological and ecological performance optima, and population refuges	159
Chapter 6	
SUMMARY AND CONCLUSIONS	162
VALUE OF THE STUDY: SPECIFIC AND GENERAL CONCLUSIONS	162
SYNTHESIS: <i>G. crinita</i> POPULATIONS IN THE PAST, PRESENT & FUTURE	166
SUMMARY OF CONSERVATION RECOMMENDATIONS	173
APPENDIX I	
SOURCES OF INFORMATION ON <i>Gentianopsis crinita</i>	175
APPENDIX II	
SPECIES IN <i>Gentianopsis crinita</i> SITES	177
REFERENCES	180

LIST OF TABLES

1.1	Summary of observations and experiments to study <i>G. crinita</i>	17
3.1	Responses of <i>G. crinita</i> and <i>D. carota</i> to treatments in clearings	47
3.2	Statistical analyses of treatment effects in clearings	48
3.3	Responses of <i>G. crinita</i> and <i>D. carota</i> in the scrub	53
3.4	Comparison of species' performance in scrub and clearings	57
3.5	Comparison of soil characteristics in scrub and clearings	59
3.6	Summary of responses to disturbance and competition	60
3.7	Mean numbers of seedlings emerging per plot at the Radio Lab	69
3.8	Comparison of emergence between moss and bare ground	69
3.9	Survival of seedlings in vegetation, moss, and bare ground	71
4.1	Reproductive output of <i>G. crinita</i> and <i>D. carota</i> at the Radio Lab	90
4.2	Damage to reproductive heads of <i>G. crinita</i> and <i>D. carota</i>	92
4.3	<i>G. crinita</i> and <i>D. carota</i> which did not produce seed heads	93
4.4	<i>Endothenia</i> damage and seed dispersal	96
4.5	Reproductive output of <i>G. crinita</i> and <i>D. carota</i> at Letchworth	98
5.1	Topographic, soil and population data from 32 <i>G. crinita</i> sites	111
5.2	Aspects of <i>Gentianopsis crinita</i> sites	112
5.3	Correlation of soil characteristics from 32 <i>G. crinita</i> sites	119
5.4	Soil factors and reproductive performance in 32 sites	120
5.5	Correlations of soil, plant cover, and density at the Radio Lab	133
5.6	Soil factors and reproductive performance along the transect	136
5.7	Herbivory damage to <i>G. crinita</i> transplants	140
5.8	Soil analysis of soils used in the greenhouse experiment	144
5.9	Seedling emergence, survival, and size in 3 soil types	145
5.10	Summary of <i>G. crinita</i> and <i>D. carota</i> life history characteristics	153
6.1	Generalizations about biennials and the rarity of <i>G. crinita</i>	163
6.2	Topics for future studies on the ecology of <i>G. crinita</i>	165

LIST OF FIGURES

2.1	Sites where detailed studies of <i>Gentianopsis crinita</i> were made	20
2.2	Range of <i>Gentianopsis crinita</i> in North America	23
2.3	Relative abundance and conservation status of <i>G. crinita</i>	25
2.4	Morphology of <i>Gentianopsis crinita</i>	27
2.5	Morphology of <i>Daucus carota</i>	31
2.6	Weekly rainfall at the Ithaca weather station	36
2.7	Weekly rainfall at the Portageville weather station	37
3.1	Layout of the experiments in the Natural Area	41
3.2	Experimental design used in the clearings in 1987-89	42
3.3	Example of layout of plots in the scrub experiment	44
3.4	Timing of emergence of <i>D. carota</i> and <i>G. crinita</i>	49
3.5	Emergence of <i>G. crinita</i> and <i>D. carota</i> in all treatments	55
3.6	Establishment of <i>G. crinita</i> and <i>D. carota</i> in all treatments	56
3.7	Frequency distribution of rosette diameters of <i>G. crinita</i>	58
3.8	Seedling numbers of <i>G. crinita</i> and <i>D. carota</i> in 3 microhabitats	68
3.9	Range of <i>G. crinita</i> relative to the forest zone	74
3.10	Distribution of seeds around <i>G. crinita</i> plants	79
3.11	Potential dispersal distances of <i>G. crinita</i> seeds	80
4.1	Pattern of reproductive output of <i>G. crinita</i> and <i>D. carota</i>	89
4.2	Mean percent seed dispersal of <i>G. crinita</i> and <i>D. carota</i>	95
4.3	Number of seeds per capsule in relation to height of <i>G. crinita</i>	99
5.1	Locations and habitats of <i>G. crinita</i> sites surveyed in New York	106
5.2	Ground cover at the 32 <i>G. crinita</i> sites	113
5.3	Calcium content and pH of soil at 32 sites	115
5.4	Particle size distributions from the rooting zone of <i>G. crinita</i>	116
5.5	<i>G. crinita</i> population size and density at 32 sites	118
5.6	Flowering <i>G. crinita</i> and <i>D. carota</i> at the Radio Lab	123
5.7	Map of densities of flowering plants at the Radio Lab field	124
5.8	Distribution of survival of <i>G. crinita</i> and <i>D. carota</i> seedlings	125
5.9	Variation in soil water potential across the Radio Lab field	127
5.10	Distribution of <i>G. crinita</i> and <i>D. carota</i> across the Radio Lab field	130
5.11	Plant cover, soil water, pH, and calcium at the Radio Lab field	132
5.12	Plant cover in relation to soil characteristics	134
5.13	Distribution, density, and survival of <i>G. crinita</i> and <i>D. carota</i>	135
5.14	Changes in soil moisture in five watering treatments	147
5.15	Effects of soil type and moisture on <i>G. crinita</i> rosette diameters	149
5.16	Effects of soil type and moisture on <i>D. carota</i> rosette diameters	150
6.1	Range of <i>G. crinita</i> in relation to the limit of maximum glaciation	167
6.2	Scenarios of possible future changes in the range of <i>G. crinita</i>	172

CHAPTER 1

INTRODUCTION

Why are some plant species less abundant than others? This is a fundamental question for plant ecologists to answer, but so far it has received much less attention than the study of the population ecology of individual species. Among the few studies that directly address the question, there has been notable work by Grubb and his colleagues (for example, Grubb, Kelly & Mitchley 1982, Grubb 1986, Mitchley & Grubb 1986) and Rabinowitz and her co-workers (for example, Rabinowitz 1981, Landa & Rabinowitz 1983, Rabinowitz, Rapp, Cairns & Mayer 1989). A better understanding of relative abundance or scarcity is not only of interest to ecologists, but also is extremely important for conservation managers who are attempting to preserve rare species in natural or semi-natural vegetation. However, the complexity of all the potentially relevant ecological factors that might influence plant species rarity often appears to be overwhelming, particularly since the available resources for research are usually limited.

The goals of my project were to examine the question of why one particular plant species is relatively rare and to do this effectively by adopting a new kind of comparative life history approach. I decided to use this approach to focus on the critical factors that affect the relative scarcity of the fringed gentian, *Gentianopsis crinita* (Froel.) Ma (nomenclature follows Iltis 1965 and Mitchell 1986). This species is a herbaceous biennial plant native to North America. *Gentianopsis crinita* is in urgent need of conservation action, yet very little is known about why it is scarce. I refer to it in my thesis by its full name or as *G. crinita*.

Although any individual species may have a unique relationship to various controlling factors, attempts have recently been made to find patterns by describing the general characteristics of rare plant species (Rabinowitz 1981, Harvey 1985, Rabinowitz et al. 1986, Hodgson 1986a). One underlying pattern may be that of shared life history traits, for example characteristics such as reproductive output and survival in the vegetative stage. Harvey (1985) tried to make generalizations about the life history traits of rare species, although he acknowledged that very limited data were available and was only able to reach tentative conclusions about one life history group, namely herbaceous perennials.

My approach also attempts to use patterns of life history traits to understand rarity, but I have tackled the problem from another direction. Instead of considering the meagre information available on rare species from different life history groups, I use generalizations from existing information about one particular life history group, namely biennials, as a framework to study the complex question of why *G. crinita* is a rare biennial. "Rarity" can be defined in several ways, for instance it may describe species that have restricted ranges and few populations, or species that are widely distributed but have low local population sizes (Drury 1980, Harper 1981, Rabinowitz 1981). The components of *G. crinita*'s rarity that I examined were the infrequent occurrence of populations in the landscape, their relatively small size and limited spatial extent. For the purposes of my project, the definition of "biennial" follows that given by Kelly (1985). Biennials are monocarpic, i.e. flower only once before dying. Two kinds of biennials have been distinguished by Kelly: he termed one type a "strict biennial" because it takes two years to flower, while he called the other kind a "facultative biennial," as it can take two or more years to flower. My study refers to both categories, which are also sometimes collectively known as monocarpic or semelparous perennials (Silvertown 1983, 1984). The biennial life history group was a suitable one to choose for my approach because it has been the subject of several theoretical ecology papers and there have been many empirical studies of common biennial species. Also there is evidence (Hodgson 1986b and data in Perring & Farrell 1983) that short-lived monocarpic species are under greater threat than polycarpic perennials (which flower several times

before dying) so there is a special need to improve understanding of the ecology of rare monocarpic plants. Hodgson, in his study of the flora of the Sheffield area in central England (1986b), found that obligately monocarpic groups of species within families had a higher incidence of rarity than polycarpic groups in these families. Among plants in the Red Data Book for Britain, which lists rare species present in 15 or fewer of the 2980 10x10 km squares of the Ordnance Survey grid that covers the country (Perring & Farrell 1983), I found that a significantly greater proportion of short-lived plants (75% of annuals and biennials) were described by Perring and Farrell as undergoing serious declines in frequency (i.e. more than 33% decline, the baseline for most species being around 1970), compared to the proportion of polycarpic perennial species that were declining (50%; $\chi^2 = 10.05$, $p < .005$).

Life history theory suggests that different types of life history evolve under different sets of environmental conditions (Murphy 1968, Stearns 1977). Species that share similar life history traits therefore tend to occur in similar habitats (Grime 1977, Southwood 1977, Greenslade 1983, Begon 1985). With regard to biennial plants, several generalizations can be derived from existing studies to describe a model of a "successful" biennial life history and the habitats commonly occupied by biennials. These generalizations can then be used to examine the factors that critically limit the abundance of *G. crinita*.

The following generalizations were drawn from the literature:

- a. Biennials appear in early to mid-successional habitats before the development of forest cover, and populations may persist for some considerable time through the early to mid-successional period (Bard 1952, Pickett 1982). In these open habitats, biennials may occur in local patches of bare ground or in more or less closed swards of herbaceous vegetation (Grubb 1976, Gross 1980, Gross & Werner 1982, Thompson 1984, Goldberg 1987).
- b. Biennials are successful at colonizing intermittently available open habitats (Hart 1977, Silvertown 1983, 1986) and have efficient seed dispersal in space or long-lived buried seed (Grubb 1976, Harper 1977, Gross & Werner 1982, de Jong et al. 1987, Grime et al. 1988).
- c. Biennials can successfully compete with annuals or polycarpic perennials because they have (i) high reproductive output and/or (ii) good survival in the vegetative stage (Hart 1977, Harper 1977, Silvertown 1983, Klinkhamer & de Jong 1983, Thompson 1984, Klemow & Raynal 1985, de Jong & Klinkhamer 1988).

To make a proper assessment of the significance of different factors operating at particular stages of *G. crinita*'s life history, a direct comparison with a common biennial was required. Bradshaw (1987) emphasized the fundamental importance of making direct comparisons in ecological studies. He pointed out that while studies of single species are very prevalent in the ecological literature, they have limitations. To understand the significance of such studies they have to be indirectly compared with observations on other species, usually made by different methods, in different locations or at different times. Direct comparisons were always a feature of Rabinowitz's work and led to illuminating conclusions about rarity (e.g. Rabinowitz 1978a, Rabinowitz et al. 1984, Rabinowitz & Rapp 1985, Rabinowitz et al. 1989).

Fortunately, a very common biennial, *Daucus carota* L. (wild carrot or Queen Anne's lace), occurs in the same habitats as *G. crinita* in North America and therefore could be used as a direct comparison. It has been well studied by ecologists in North America, in comparative work on the ecology of the common biennials found in old fields (e.g. Gross 1981, Gross & Werner 1982, Goldberg 1987), and in investigations of European chalk grassland where the mix of species sometimes included biennial members of the Gentianaceae (Grubb 1976, Verkaar et al. 1983a, Verkaar & Schenkeveld 1984a). In my thesis I refer to *Daucus carota* either by its full name or as *D. carota*.

The generalizations a) to c) outlined above provide the themes around which the chapters of my thesis are organized. After a background chapter on the biology of the two study species and descriptions of the study sites (Chapter 2), the next three chapters examine the three generalizations and the hypotheses that can be derived from them to explain why *G. crinita* is rare. A summary of the findings and comments on the wider implications of the project for the understanding of rarity, and for the conservation of the species, conclude the thesis.

The project involved a great variety of field observations and experiments in a number of locations and at different times during the period 1986 to 1990, as well as greenhouse experiments carried out at Cornell University over this time. Table 1.1 summarizes how all these activities were related to the generalizations about biennials and the tests of hypotheses that are described in Chapters 3, 4 and 5. Observations were made on both species in most cases. Aspects of seed dispersal of *D. carota* that had been studied in detail previously (Holt 1972, Lacey 1978, Roberts 1986) were not included. A few of the observations on habitat characteristics, incidence of herbivory, and reproductive output were judged to be necessary only for *G. crinita*, given the time constraints on the project.

Table 1.1. Summary of observations and experiments designed to study the critical factors influencing the rarity of *G. crinita*. The Radio Lab field and the Natural Area are study sites near Ithaca, central New York. The Letchworth site is in Letchworth State Park, western New York. The greenhouse and laboratory experiments were located at Cornell University, Ithaca. Unless otherwise specified, observations were made on both *G. crinita* and *D. carota*.

a.	<i>Generalization:</i>	Biennials appear in early to mid-successional habitats and may persist for some time (Chapter 3).	
	<i>Hypothesis:</i>	<i>G. crinita</i> can only survive through a short part of a successional change from bare ground to forest.	
<u>Test</u>		<u>Location</u>	<u>Time period</u>
Field experiments to simulate different degrees of disturbance and competition. Seed sown in 7 treatments in open clearings and scrub; recording of seedling emergence, survival of vegetative plants and reproductive output.		Natural Area	Fall '87-Fall '89
	<i>Hypothesis:</i>	<i>G. crinita</i> is restricted in abundance by a scarcity of suitable microhabitats for colonization and regeneration, in the successional habitats where it can survive.	
<u>Test</u>		<u>Location</u>	<u>Time period</u>
Field experiments and observations on seedling emergence and survival in 3 microhabitats in plots with sown or "native" seed.		Radio Lab field & Letchworth	Fall '86-Fall '89

b.	<i>Generalization:</i>	Biennials are successful at colonizing intermittently available habitats and have efficient seed dispersal in time or space (Chapter 3).	
	<i>Hypothesis:</i>	<i>G. crinita</i> has limited colonizing ability because of poor seed dispersal capabilities.	
<i>i. <u>Poor seed dispersal in time</u></i>			
<u>Tests</u>		<u>Location</u>	<u>Time period</u>
Clearance of scrub and ground disturbance in area where <i>G. crinita</i> once occurred. Recording of any flowering <i>G. crinita</i> , which may have originated from a buried seed bank.		Natural Area	Fall '87-Fall '90
Collection of soil samples from scrub where <i>G. crinita</i> once occurred to see if any <i>G. crinita</i> seedlings emerged from a buried seed bank.		Natural Area	Fall '87-Summer '88

Table 1.1. (continued)

i. Poor seed dispersal in time (continued)

<u>Tests</u>	<u>Location</u>	<u>Time period</u>
Recording seedling emergence rates in successive years from seed sown in clearings and scrub, and for <i>G. crinita</i> only, in an open old field, to investigate if rates decline substantially over time.	Natural Area	Spring '88-Fall '89
	Radio Lab field	Spring '87-Summer '89
Recording seedling emergence from seeds sown before and after stratification of varying lengths to investigate length of seed dormancy.	Greenhouse	Fall '88-Fall '89

ii. Poor seed dispersal in space

<u>Tests</u>	<u>Location</u>	<u>Time period</u>
Estimation of pattern of wind dispersal of <i>G. crinita</i> seeds using sticky seed traps in the field, and calculation of terminal velocity of <i>G. crinita</i> seeds in the lab.	Radio Lab field	Fall '89-Spring '90
	Laboratory	Fall '89
Assessment of potential for water dispersal by recording seedling emergence after seeds floated or submerged in water. Study of effect of moss on movement of <i>G. crinita</i> seeds.	Greenhouse	Fall '88-Fall '89

c. (i) *Generalization:* Biennials have a high reproductive output (Chapter 4).

Hypothesis: The relative scarcity of *G. crinita* is due to the low reproductive output of adult plants.

<u>Tests</u>	<u>Location</u>	<u>Time period</u>
Recording of production of flowers or umbels, fruits and seed heads, and losses of these reproductive heads.	Radio Lab	Fall '87, Fall-Winter '88, Fall-Winter '89
Counting of seed numbers per flower or umbel and estimation of seed weights.	Radio Lab: Letchworth:	Fall '87,'88,'89 Fall '88, '89
Recording timing of reproductive events.	Radio Lab, Letchworth, & Natural Area	Fall '87-'89

Table 1.1. (continued)

- c. (ii) *Generalization:* Biennials have good survival in the vegetative stage (Chapter 5).
- Hypothesis:* In unwooded landscapes the survival, growth and potential reproductive output of *G. crinita* in the vegetative stage are limited by a narrow range of soil conditions.

Tests	Location	Time period
Survey of 32 sites that had <i>G. crinita</i> populations, to record habitat features, population size, extent and relative reproductive performance. (<i>G. crinita</i> only)	New York State	Fall '89
Recording of distribution abundance, survival and size for both species, and for <i>G. crinita</i> only, reproductive performance, in relation to soil factors, plant cover and herbivory along a transect within a <i>G. crinita</i> site.	Radio Lab field	Spring-Fall '89
Recording of seedling emergence, survival and size from seed transplanted to locations with few or abundant "native" individuals within a <i>G. crinita</i> site, in relation to soil factors, plant cover and herbivory in transplant locations.	Radio Lab field	Fall '88-Fall '89
Recording of herbivory on first- and second-year plants of <i>G. crinita</i> transplanted from the greenhouse to an existing <i>G. crinita</i> site and a site previously without <i>G. crinita</i> .	Radio Lab field, Turkey Hill old field	Summer-Fall '89
Recording of seedling emergence, survival and growth in 3 soil types.	Greenhouse	Fall '88-Summer '89
Recording of growth of first-year plants in 5 moisture treatments ranging from dry to waterlogged.	Greenhouse	Fall '88-Summer '89
Recording of seedling emergence, survival and growth in moist or waterlogged substrates.	Greenhouse	Fall '89

CHAPTER 2

BIOLOGY OF *Gentianopsis crinita* AND DESCRIPTIONS OF THE STUDY SITES

INTRODUCTION

To provide the context for my detailed ecological study of *Gentianopsis crinita*, a brief review of existing knowledge about the species and its relatives is given in this chapter. Also included is a summary of the biology of *Daucus carota*, the common biennial chosen as a comparison for *Gentianopsis crinita*. The chapter concludes with descriptions of the main study sites. All of them lie in New York State; two are near Ithaca and the other is a hundred miles (160 km) to the west in Letchworth State Park (Fig. 2.1).

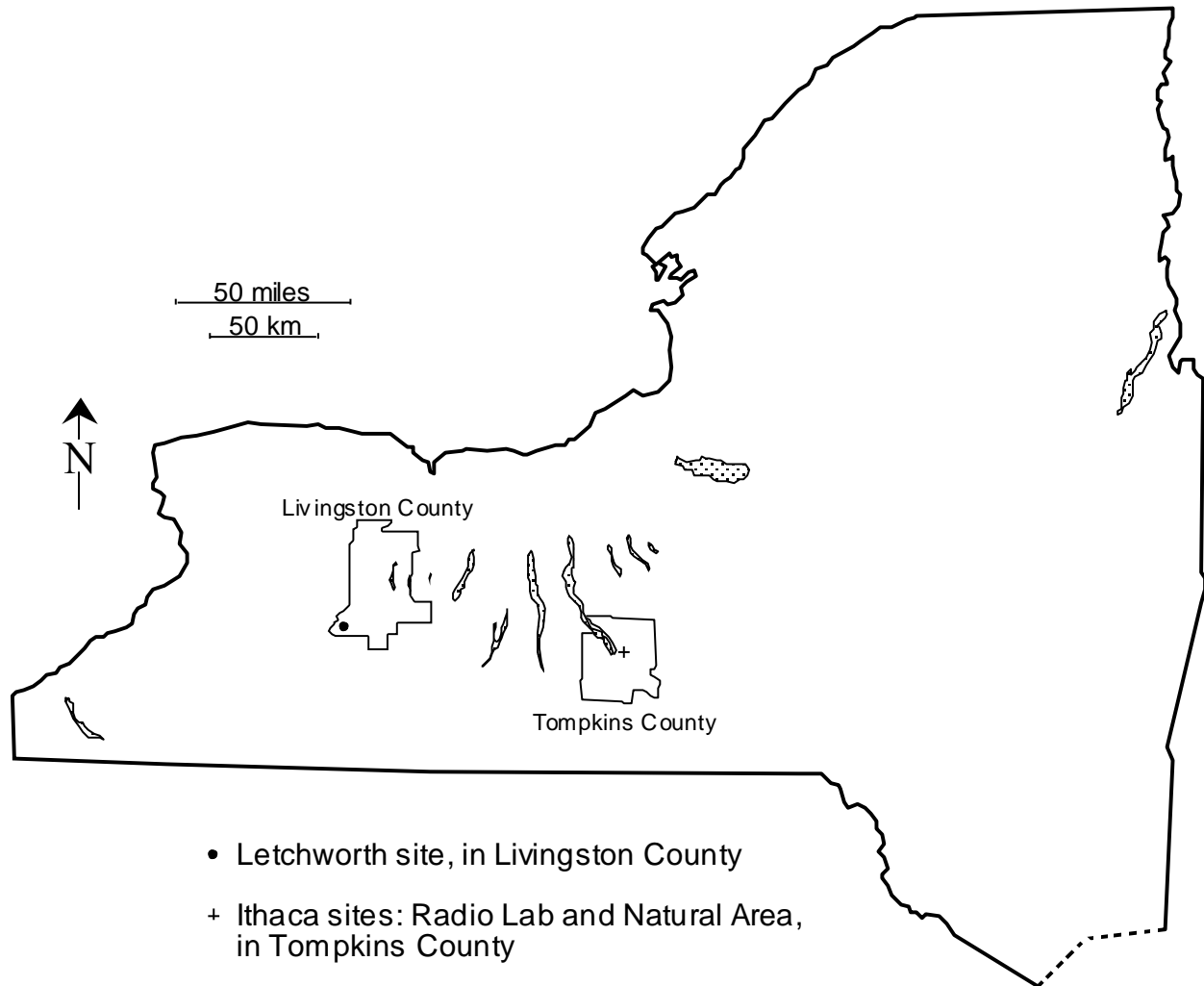


Fig. 2.1. Location of sites where detailed studies of *Gentianopsis crinita* were made between 1986 and 1990 in New York State.

BIOLOGY OF *Gentianopsis crinita* (Froel.) Ma

Taxonomy

There is no consensus about the taxonomy of *Gentianopsis crinita*. Opinion is divided about the status of the genus and the species. Until the late 1950's it had been included in the genus *Gentiana*. My study follows the definitions in Iltis (1965), who supported the establishment of the separate genus *Gentianopsis* by Ma in 1951. Iltis included *G. crinita* in this genus, which he argued is distinctive, based on morphological characters such as angular, papillose seeds, distribution of ovules in the placentae, and the frequently fringed or toothed corolla lobes. Gillett (1957, 1963) placed fringed gentians in the genus *Gentianella* (as subgenus *Eublephis*) and his classification is used by Canadian botanists (G. Argus, Canadian Rare Plant Project, Ottawa, Ontario; pers. comm.).

A number of *Gentianella* species occur in Europe, including a biennial fringed gentian, which is known as *Gentianella ciliata* (L.) Borkh. It has recently been rediscovered in Britain, where it occurs in only one locality (Knipe 1988). Wood and Weaver (1982) regarded this species as *Gentianopsis ciliata*, following Ma's classification, although they noted that *Gentianella* is the closest ally of *Gentianopsis*.

Gentianopsis procera is closely related to *G. crinita*. However, Iltis maintained that *G. crinita* is a distinctive species and relatively stable in morphological characters while *G. procera* is variable and includes other species or subspecies such as *G. victorinii* and *G. macounii*. This assessment was supported by Wood and Weaver (1982). Gillett regarded Iltis' *G. crinita* as one of four subspecies within "*Gentianella crinita*," i.e. *Gentianella crinita* subsp. *crinita*. The others are subsp. *procera*, subsp. *victorinii*, and subsp. *macounii*.

Historical background

Plants in the family Gentianaceae have attracted interest over a very long period of history, primarily because of their medicinal value. The name of the family is taken from Pliny the Elder's writings (ca. A.D. 77). "It was a king of the Illyrians named Gentius who discovered gentian..." (Jones 1963b). In his Natural History, Pliny listed numerous remedies that employed gentians, even including one for rabies. Pharmacological investigations have continued (Weber 1984), for instance the recent identification of various flavonoids and xanthenes in some species (Ghosal & Jaiswal 1980, Van der Sluis & Labadie 1981). However, only anecdotal reference appears to have been made to the medicinal use of American gentian species, including *Gentianopsis crinita* (Graves et al. 1910).

Since the 1800's *Gentianopsis crinita* has attracted attention for aesthetic rather than practical reasons. Its beauty was praised in poetry, notably by William Cullen Bryant (about 1832) and Emily Dickinson (about 1862). Thoreau, writing in the 1850's (published 1906), recorded in his journals some observations he made about the plant at Concord, Massachusetts. He commented on its rarity and emphasized the transience of the flowering adult plants. He noted that they were visible for only a few weeks before the first severe frosts of the fall, and concluded that "It [*G. crinita*] came very near not being an inhabitant of our latitude, perhaps our globe, at all." He also described the intense blue color of the flowers and referred to Bryant's poem. It seems that many other people were inspired by the poem too, but with unfortunate consequences (Hansen 1923). Flowering stems were picked on a large scale, apparently even being sold on street corners in cities (Hansen 1923). By the early years of the twentieth century concern was being expressed about the plant's decline in abundance owing to these depredations (Sempers 1905b, Britton 1916, Hansen 1923, Matschat 1933). Around the same time and partially due to this concern, horticulturalists became interested in propagating *Gentianopsis crinita* (Sempers 1905b, Britton 1923, Norton 1923).

Comments on the difficulties of raising the plant from seed have been made since the middle of the nineteenth century to the present day (Torrey 1843, Bruce 1976). Sanders (1986), writing for the New York Times newspaper, summed up the public perception of the plant as "probably the fussiest, least predictable and hardest to tame of well-known wildflowers." Around the beginning of the twentieth century, Doubleday, Page and Company offered a gold medal to the first person to successfully propagate the plant in a garden (Stratton-Porter 1925). The medal was awarded in 1905 (Britton 1925). Several attempts were successful using traditional techniques of sowing seeds in pots, then transplanting the young plants to larger pots or into the garden. Soil types usually included loam and/or "moss" (sometimes peat moss) in quantity (Norton 1925, Hedden 1931, Nearing 1932, Matschat 1933). A number of comments were made about the need for neutral or alkaline conditions (Sempers 1904, Britton 1924, Matschat 1933) and moist substrates, though sometimes this requirement was qualified by specifying a moist but not saturated growing medium (Sempers 1905b, Britton 1924, Norton 1925, Abbey 1930, Matschat 1933, Giersbach 1937).

Sowing seed 'in the wild' or directly in the garden was also sometimes successful (Britton 1923, Norton 1925). Norton actually sent many packets of seeds to people who responded to his suggestions about sowing seed in this way, including Mrs. Coolidge, who scattered seeds in the White House grounds (Norton 1925). Others introduced seeds to new localities on their own initiative, for instance in northern and western New York State (G. Chase, naturalist from Saranac Lake, New York; R. Pappert, manager of the Elizabeth Slater Preserve for the Bergen Swamp Preservation Society and the Burroughs-Audubon Nature Club; pers. comms.). As a result the species might now be slightly more frequent in suitable, accessible habitats than without such intervention, although flower picking may have removed it from other accessible native sites. The impact of human activity on the distribution and abundance of *G. crinita* is considered further later in this chapter and in Chapters 5 and 6. Despite the reported difficulties of cultivation, seed is now commercially available to gardeners from wildflower seed companies (D. Winkler, Cornell University; pers. comm.).

Apart from two studies of seed germination in the laboratory (Giersbach 1937, Farmer 1978) there appears to have been no ecological investigations of *G. crinita*. Among closely related biennial or annual *Gentianella* species there have been a fair number of studies of these plants in chalk grassland in Britain and The Netherlands. Detailed discussion of aspects of previous work relevant to my study will be found in Chapters 3-5.

Distribution, abundance and conservation status of *G. crinita*

The range of *G. crinita* is restricted to North America, where it occurs from Maine to Manitoba and Quebec to Georgia (Fig. 2.2). Very broadly, the two climatic zones which cover this range are warm temperate and cool temperate rainy climates (Fullard et al. 1981). Annual precipitation can range from 500-2000 mm and from May to October between 250-750 mm, while temperatures can be – 20°C in winter and around 30°C in summer.

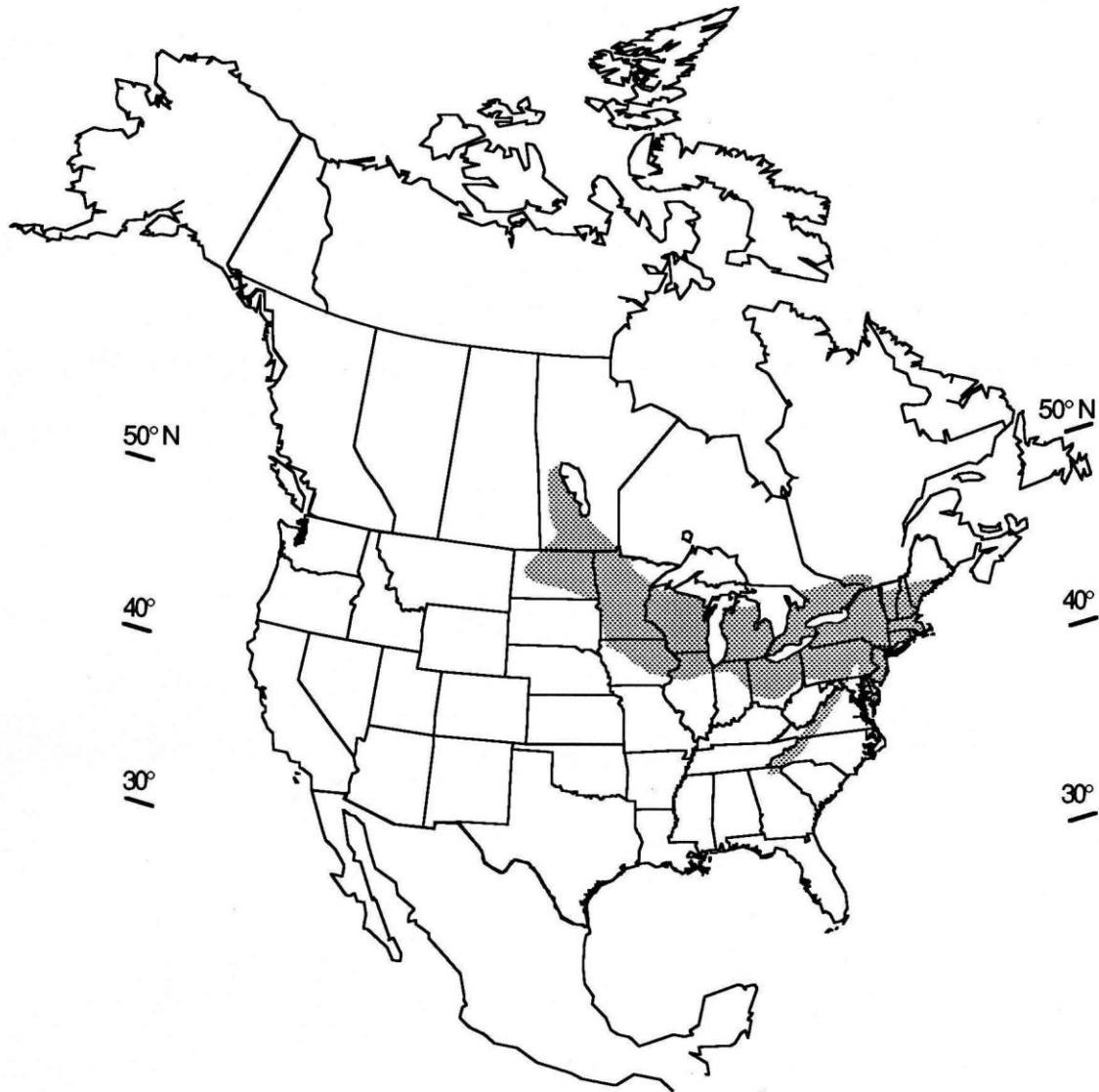


Fig. 2.2. Range of *Gentianopsis crinita* (shaded) in North America. Adapted from Iltis (1965).

Published information on the habitats where *G. crinita* is found frequently refers to features such as low-lying moist ground, usually open situations rather than wooded, and sometimes the presence of calcareous substrates (e.g. Graves et al. 1910, Wiegand & Eames 1926, Deam 1940, Ahmadjian 1979, Andreas & Cooperrider 1981). Some sources also list low-lying woods and damp thickets (Gleason 1952, Scoggan 1957, Torrey 1843).

The history of *Gentianopsis* species in eastern North America goes back at least to the late Pleistocene around 11,000 years ago. Miller (1989) found a fossil seed in sediments of that date at Columbia Bridge, Vermont. He was not able to determine whether it was *G. crinita* or *G. procera*.

G. crinita was recorded quite early in the history of European settlement of North America, for instance Jacob Green, who listed plants he saw in New York State in the 1700's, mentioned *G. crinita* (Green 1814). Torrey (1843) described the plant in his Flora of New York State. Around

Ithaca, where much of my work was done, the earliest specimen in the Bailey Hortorium at Cornell University is dated 1872. It came from Fall Creek and was collected by W. R. Dudley.

Concern about the vulnerability and decline of *G. crinita* has been referred to already, in perhaps the first instance of poetry being regarded as a conservation threat! However Matschat (1933) also mentioned habitat loss, in this case the drainage of a marsh. More recently Iltis (1965) and Seymour (1982) have referred to the decline in abundance of the species in the midwest and northeastern U.S.A. Iltis (pers. comm.) notes that the decline in Wisconsin has continued up to the present, probably largely due to habitat loss. At a local scale around Ithaca *G. crinita* appears to have declined over the last 20 years or so (F. R. Wesley, Natural Areas Committee, Cornell University, pers. comm.).

To try to get an up to date picture of the abundance of *G. crinita*, all State Natural Heritage Programs thought to be within its range were contacted during the project (see Appendix I). In four states, South Dakota, South Carolina, Kentucky, and Tennessee, *G. crinita* had not been recorded. For the remaining 23 states, Program staff supplied, where possible, comments on the relative abundance of the plant, in terms of frequency of population localities, and its conservation status, whether it was thought to be declining, and probable reasons for its decline. The information on abundance and conservation status was supplemented by references to *G. crinita* in published material, especially floras (see Appendix I), and my knowledge of the plant in New York State. The results are summarized in map form in Figure 2.3. As can be seen from the map, *G. crinita* was regarded as endangered or threatened in several states, while in two states it was extinct or had a historical record only (Delaware and West Virginia). The midwestern states of Wisconsin, Michigan and Indiana appear to be its 'stronghold' and center of its distribution. In these states it was reported to be at best locally common, and then only in parts of each state. Even in *G. crinita*'s 'stronghold' the wetland habitats in which it occurs were considered to be under threat. In 12 states, *G. crinita* was thought to be declining due to habitat loss, particularly drainage of wetlands and regrowth of forest on abandoned agricultural land. The additional threat posed by flower picking was only mentioned for two states. Overall *G. crinita* was thought to be declining or its habitats were under threat in 16 states. It was thought to be endangered in two of the remaining five states in which it still occurred because populations were so few in number.

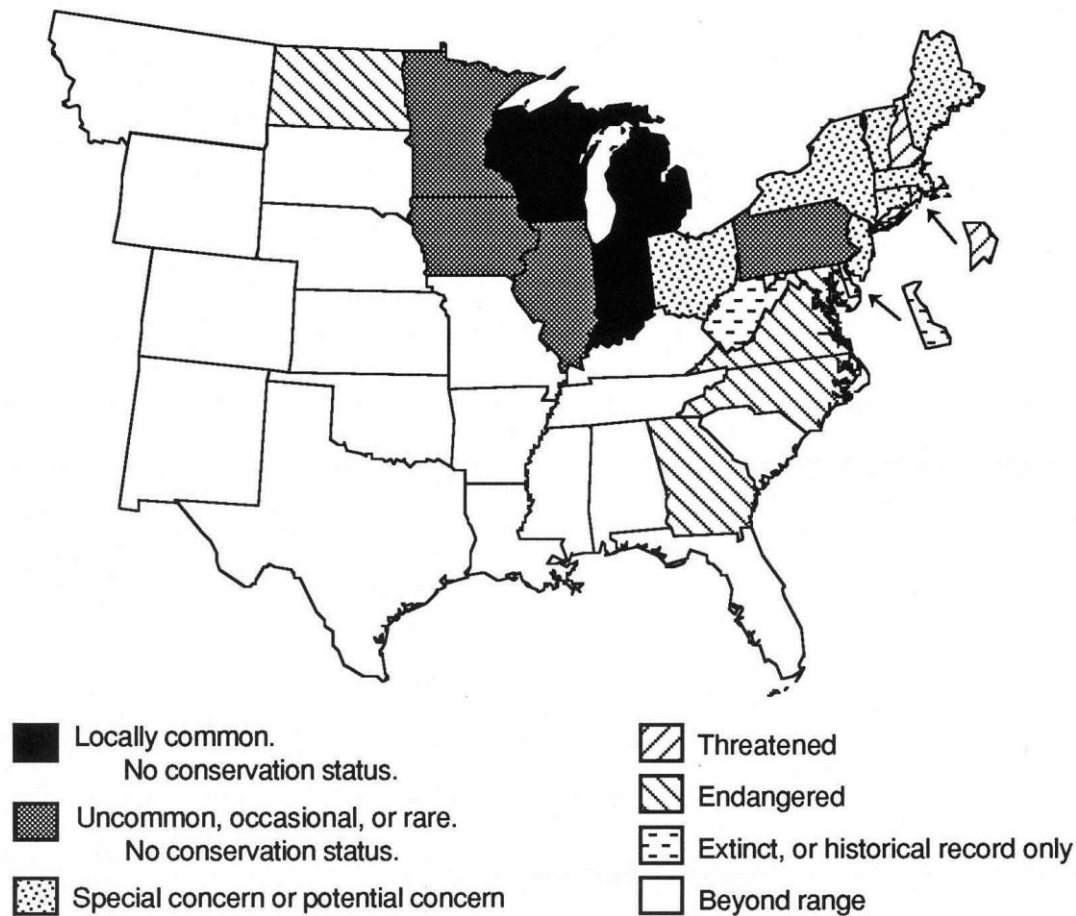


Fig. 2.3. Relative abundance, i.e. frequency of populations, and conservation status of *Gentianopsis crinita* in the United States of America. The map is based on information received from State Heritage Programs and records in state floras (listed in Appendix I) and my knowledge of *G. crinita* in New York State.

The categories of "extinct, or historical record only," "endangered," and "threatened" are the conservation status of the species as defined by the relevant State Heritage Program. "Endangered" and "threatened" generally have a numerical meaning in terms of numbers of populations, varying slightly from state to state, but in all cases "endangered" is less than 5 populations and "threatened" less than 20 populations where numbers are specified. The other categories represent more subjective estimates of conservation status and relative abundance of populations.

Note: In Canada, *G. crinita* is treated as a subspecies in the genus *Gentianella*, following Gillett (1957, 1963) i.e. *Gentianella crinita* subsp. *crinita*, and information on abundance is limited. The subspecies is rare in Quebec and appears to have a restricted distribution in Manitoba and Ontario (see Appendix I).

Life cycle and morphology of *Gentianopsis crinita*

In the literature, *G. crinita* has been described as a biennial and/or an annual (Britton 1924, Gillett 1963, Iltis 1965, Farmer 1978). In this study *G. crinita* behaved as a strict biennial, which Kelly (1985) defined as a plant that flowers only in its second year. He contrasted this behavior with that of facultative biennials that can remain vegetative for two or more years before flowering. *G. crinita*'s life cycle in the New York State study sites for the duration of this project was the same as the two strict biennials, *Linum catharticum* and *Gentianella amarella*, studied by Kelly (1989a, b, c) in southern England. As with these species, *G. crinita* germinated in the spring, grew vegetatively during that year and in the following spring, then flowered late in the second summer season. Seed produced during the fall and early winter was dormant and the highest proportion of seeds to germinate in two successive springs did so in the spring immediately following dispersal. Thus the generation time from seedling stage to seedling stage was generally 24 months.

Kelly (1989a) noted that strict biennials can behave as annuals in other localities, for instance *Linum catharticum* in the Netherlands. It is not clear on what basis the published reports of *G. crinita* behaving like an annual were made. They may not be correct, as the first year rosettes, which are often tiny, can be extremely difficult to find by casual inspection.

The morphology of the different stages of *G. crinita*'s life cycle as observed in this project are illustrated in Figure 2.4. At the study sites in New York State most seedlings emerged in May. The two cotyledon leaves of a seedling (Fig. 2.4a) were ovate to somewhat spoon-shaped in outline when fully expanded. They did not shrivel early in the growing season but remained part of the rosette (Fig. 2.4b, c). In late November to early December a central bud usually became evident and during the winter the rosette leaves shrivelled (Fig. 2.4d). In the following spring the bud gave rise to new leaves, generally in April. The stem then began to elongate and flower buds appeared around the end of July or early August. Flowering occurred from late August into November, but mainly during September and October (Fig. 2.4e, f). The seed capsule split open at the top as soon as seeds were ripe (Fig. 2.4g). The seeds were dark brown in color when ripe (Fig. 2.4h) and were shed over the period from late fall to the following spring.

Below ground, the slender white or translucent roots of the plant appeared to be rather sparsely branched and brittle. After the first year, the main root immediately below the rosette became somewhat thickened (Fig. 2.4c). The association of mycorrhizal fungi with roots of *G. crinita* was not studied. However, it would not be surprising to find that such an association exists, as it now seems that most plant species are infected with these fungi (Tester et al. 1987) and mycorrhizae occur quite widely in the Gentianaceae (Jacquelinet-Jeanmougin & Gianinazzi-Pearson 1983, Weber 1984, Demuth et al. 1991). Weber (1984) found vesicular-arbuscular mycorrhizae in 35 out of 50 members of the family. *Gentianella amarella* was one of three species of Gentianaceae found to have vesicular-arbuscular mycorrhizae in a study of chalk grassland plants in Britain (Gay et al. 1982).

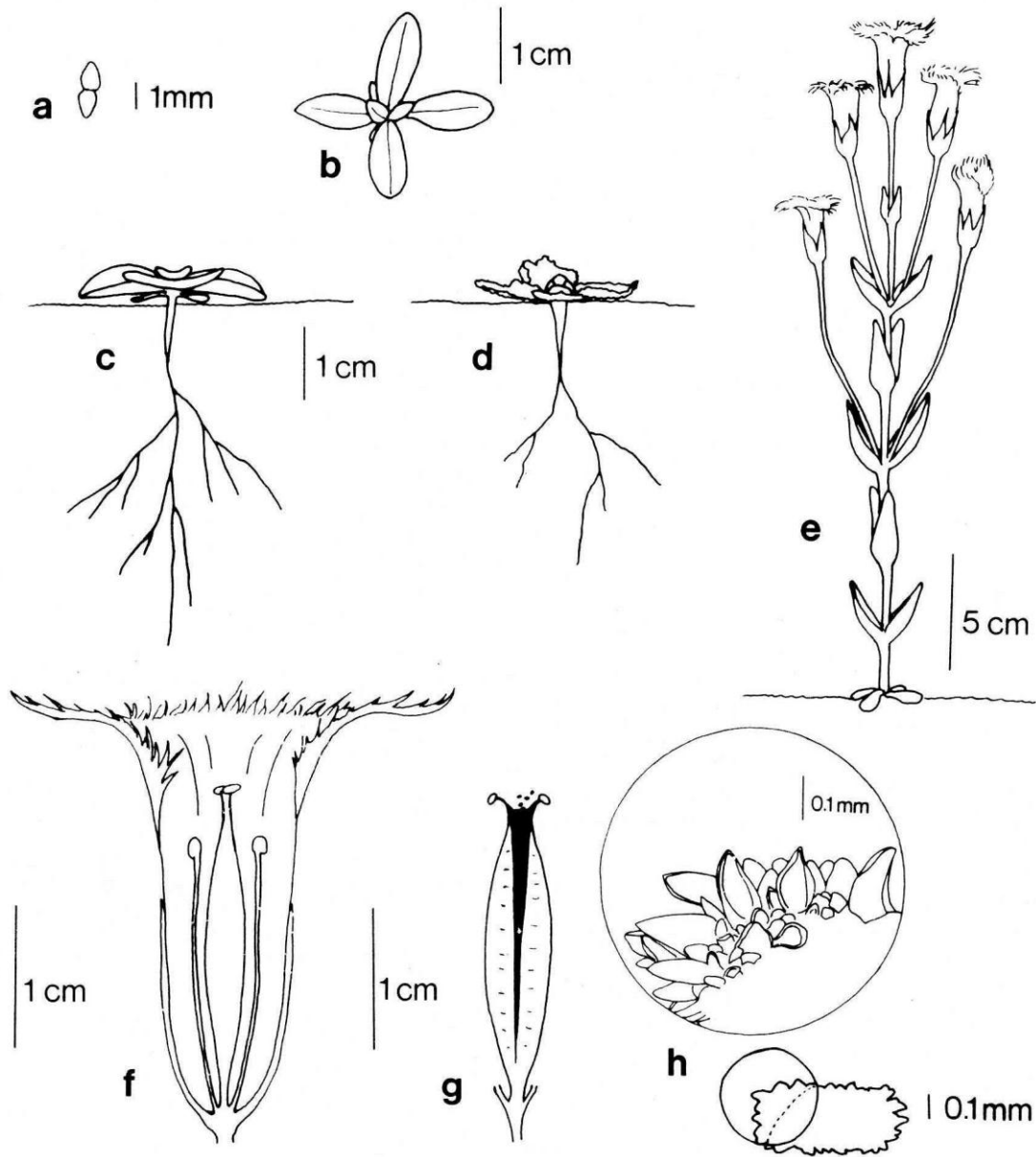


Fig. 2.4. Morphology of *Gentianopsis crinita*. I based these illustrations on my observations and photographs.

- a) Seedling at the cotyledon stage viewed from above.
- b) Rosette after one season's growth viewed from above.
- c) Rosette after one season's growth viewed from the side.
- d) Rosette at the end of the first year, showing central bud and shriveled rosette leaves, viewed from the side, at same scale as in (c).
- e) Flowering plant in the second year.
- f) Section of flower showing arrangement of pistil and stamens.
- g) Capsule beginning to disperse seed. Note: the capsule is usually partly enclosed in the withered remains of the calyx and corolla.
- h) Close up of seed and its surface papillae (circled inset).

Floral biology

From some limited observations, which are briefly described below, it appeared that the *G. crinita* populations studied were not obligately outcrossing but did require insect pollinators to move pollen onto the style to enable viable seeds to form. Examination of the structure of the flower (Fig. 2.4f) revealed that the anthers were situated below the style and both were enclosed by the corolla. Thus insects were thought to be the agents by which pollen is transported, rather than a combination of wind and gravity. Honey bees and bumblebees were regularly seen visiting the flowers, but other insects might also have played a role.

To test whether insect pollinators were needed to enable seeds to develop, a small experiment was carried out at the Radio Lab study site near Ithaca. In early September 1987, nylon mesh bags measuring 10 cm by 10 cm, with a mesh diameter of 1 mm, were placed over flowers that had not quite reached the petal-opening stage in order to exclude most potential pollinators. One flower from each of 20 plants was "bagged" and another flower from each of these plants was marked with thread but left "unbagged." Some heads were lost to insect or mammal herbivores. Remaining seed capsules were collected in mid-October. Of the 13 capsules remaining of each type, 11 of the capsules from bagged flowers contained relatively small seeds compared to the "normal" size of seeds in 11 of the capsules from unbagged flowers. Only 2 capsules from the 13 unbagged flowers had abnormally small seeds. Examination of seeds from a sample of 3 representative pairs of capsules showed that capsules from bagged flowers, which had seed size apparently typical of the 11 capsules with relatively small seeds, contained seeds ranging in average weight per seed from 0.0186 to 0.0191 mg. The relatively larger seed from the 3 unbagged flowers from the same 3 plants was about 5-10 times heavier (0.0695 - 0.1000 mg per seed).

At the end of November 1987, 150 seeds from each member of 5 pairs of bagged and unbagged flowers from the same plants were sown separately in ten 20 by 20 cm plots in the Radio Lab field, and 5 unseeded control plots were also demarcated to see if any natural seed input occurred in this part of the field. When the plots were inspected in the third week of June 1988 no seedlings were found in either the control plots or the plots that had been sown with seed from the bagged flowers, while a total of 56 seedlings were found in plots sown with seed from unbagged flowers. These observations suggest that pollinators larger than 1 mm in size are generally needed to ensure that viable seed develops.

In 1988 a test of the self-compatibility of *G. crinita* was made in a similar way but this time 11 plants were marked. Mesh bags were put over 2 flowers on each plant before they opened. Once open, one flower of each plant was fertilized by hand with pollen from the same flower while the other was fertilized with pollen from the nearest neighboring plant. This was done to simulate the observed pattern of movement of bees that visited flowers. In mid- to late-November 1988, capsules were collected from the 8 pairs of bagged heads that remained. The others had been lost to insect or mammal herbivores. From each capsule, 125 seeds were sown in batches of 25 seeds in 5 pots filled with Cornell mix (described more fully in Chapter 3) and overwintered on the roof of the Ecology building at Cornell University. The pots were brought into a greenhouse in spring 1989 and numbers of seedlings recorded that emerged during the main flush of germination over the two week period between 30th March and 14th April 1989. No significant difference was found in numbers emerging when selfed and out-crossed plants were compared (Wilcoxon signed rank test, $p > 0.05$). Median percent emergence was 35% for seed from out-crossed and 39% for seed from selfed plants. Seedlings of both types survived and grew apparently equally well in the greenhouse for several months. The results indicate that *G. crinita* can be self-fertile.

Senescence and the effect of frost

There is some confusion in the literature about the effect of frost on seed production of *G. crinita*. Thoreau (1906), Britton (1924) and Norton (1925) all thought that *G. crinita* was sensitive to frost presumably because the adult plant shrivelled in the fall. The latter two authors suggested that frost could reduce seed output by killing either plants or ripening seed. However Norton (1923) had previously considered that seed did not ripen before the first heavy frost. In the present study no evidence was found of seed production being affected by frost. Plants were observed to be alive and flowering into November, after snowfall and heavy frosts. In 1988 several marked plants in the Radio Lab site that had unripened seed in closed capsules in early December had dispersed apparently ripe seed by mid-January, although it is not known if the viability of this seed had been reduced.

In general, it was observed that as seeds formed and ripened the main stem and the flower stems became dried, stiff and wiry, thus holding the seed capsules above the ground, even during the snows of winter and into the following spring. However, plants which had lost all flower heads to insect or mammal herbivores remained unshrivelled for several weeks after plants with seed heads had senesced, although they then died during the winter.

BIOLOGY OF *Daucus carota*

Daucus carota L. (Queen Anne's lace, or wild carrot) is a member of the group *D. carota* subsp. aggregate *carota* described by Small (1978). The plant belongs to the family Apiaceae, previously known as Umbelliferae. The subspecies includes the cosmopolitan weedy variants of *D. carota* sensu lato (Small 1978). There can be considerable variation between individuals of the subspecies, even within one continuous population at a site. For instance hairiness of leaves and root morphology can be markedly different (Dale 1974).

D. carota was introduced into North America from Europe, probably around 300-350 years ago (Lacey 1978). The earliest record from the U.S.A. is 1739 (Dale 1974). The plant is now present throughout eastern U.S.A. and Canada, and along the west coast southward into Mexico and Central America. By 1881 it was considered to be a "serious weed" in Connecticut (Dale 1974), and it is legally classified as a noxious weed in Canada where it occurs on roadsides and in meadows and pastures (Dale & Harrison 1966, Dale 1974).

The range of *D. carota* covers a broad sweep of climatic conditions in North America, from cool temperate rainy climates to Mediterranean types with hot dry summers. Annual rainfall across these zones varies from 250-2000 mm and can be 125 mm or less in the period May to October. Temperatures range from -20°C in January to 30°C in July (Fullard et al. 1981).

Typical habitats for the plant include open situations such as abandoned crop fields and neglected pastures. It is sometimes but not always found on calcareous substrates (Dale 1974, Gross & Werner 1982, Grime et al. 1988).

The plant behaves as a facultative biennial (Kelly 1985). It sometimes may even be an annual (Lacey 1980), but no plants that have flowered have ever been observed to survive and grow the following year (Dale 1974, and my study). Seed germination can occur in autumn or spring in the midwest (Lacey 1982) but during my project most seeds germinated in spring. At my study sites cotyledon leaves of *D. carota* seedlings (Fig. 2.5a) usually shrivelled after a few weeks. During the first year's growth a thickened tap root developed together with a mass of fine roots (Fig. 2.5b). Grime et al. (1988) reported that roots can have vesicular-arbuscular mycorrhizae.

During my study, after the first growing season the rosette overwintered and new leaves appeared the following spring. If the plant "bolted" that year, the stem elongated and flower heads (umbels)

were produced around the end of June or early July. Most plants flowered during July and into August in the New York State study sites.

Generally, umbels lower down the stem develop later than the uppermost ones and some may still be immature when the plant dies (Dale 1974). The tiny flowers that make up each umbel are hermaphroditic. They are white except in some cases the central one is red-purple. *D. carota* is generally cross-fertilized, though it is self-fertile, and has a large number of pollinators including flies, bees and ants (Dale 1974).

The umbel closes over during fruit maturation, then opens out again and seeds are dispersed (Fig. 2.5c). The fruit is a schizocarp, i.e. a united ovary, which splits into two spiny mericarps or half-fruits, each of which contains one seed (Fig. 2.5d). Seed dispersal continues through the fall and over winter (Lacey 1980, and my study).

The ecology of *D. carota* has been relatively well studied in North America (e.g. Lacey 1978, Gross & Werner 1982, Gross 1984), and in studies of chalk grassland plants in Europe, together with *Gentianella* species (e.g. Grubb 1976, Verkaar & Schenkeveld 1984a, 1984b, Schenkeveld & Verkaar 1984). Detailed discussions of relevant studies are included in Chapters 3-5.

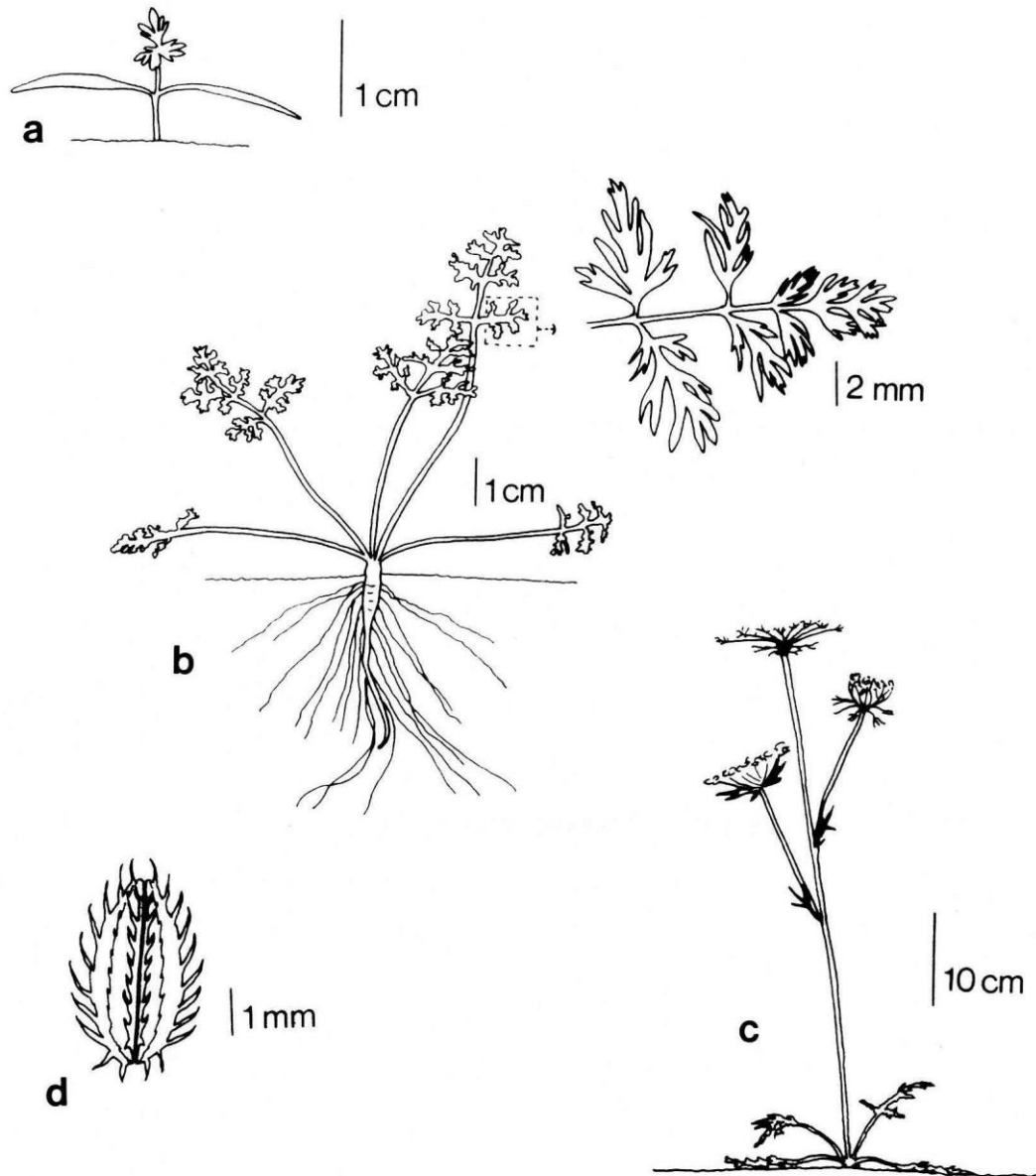


Fig. 2.5. Morphology of *Daucus carota*. I based these illustrations on my observations and photographs, and for (b) and (d) partly on close-up photographs in Small (1978).

- a) Seedling at the cotyledon stage viewed from the side.
- b) Rosette after one season's growth viewed from the side. One part of a leaf is shown in detail.
- c) Flowering plant showing head in flower (lowest inflorescence), with ripening fruit (middle), and one where seed has fully dispersed (upper). Note: usually only one or two stages are present at one time.
- d) Close up of fruit, a schizocarp which splits longitudinally into two mericarps, each of which contains one seed.

THE STUDY SITES

Description of the Ithaca study sites

Much of this project was carried out in two fields owned by Cornell University and located 6 km northeast of Ithaca, New York (latitude 42° 25' N, longitude 76° 30' W; Fig. 2.1). Both fields contained *G. crinita* populations and were conveniently close to the University. In addition, one field provided a practical conservation problem because the *G. crinita* population there had declined in recent years. This field was designated as a Natural Area and was managed by Cornell Plantations staff with guidance from the Natural Areas Committee of the University. The other field, which was situated near a Radio Laboratory research facility owned by the University, had no formal conservation designation but was recognized as an area of special value by the Natural Areas Committee and Cornell Plantations (Ostman & Marks, unpubl. report, 1990).

The Radio Lab site

The site was situated in a landscape of gentle slopes interspersed with stretches of more or less level ground, at an altitude of 339 m above sea level. The surface of the field sloped very gently southwards towards a seasonally wet watercourse which ran east to west close to the southern boundary of the field. A small bank, 0.5-1 m high and sloping down to the watercourse to the north, formed this boundary.

The soil parent material was glacial till and the soils in the area were mapped as moderately well drained Langford (= Typic Fragiochrept, USDA 1971) channery silt loam on 2-8% slopes and poorly drained Erie (= Aeris Fragiochrept, USDA 1971) channery silt loam on 3-8% slopes (USDA 1965). Puddles of standing water were sometimes present on the site during wet spring or fall weather, and were particularly noticeable near the watercourse, which was only dry in midsummer to early fall. The soil was generally shallow (5-10 cm depth) and stony over rocks or hardpan. In places a thin organic layer (1-2 cm) was present at the top of the soil profile. Soil chemistry analyses, described further in Chapter 5, showed that pH, measured on dry soil, ranged from 6.2 to 8.3 across the field from north to south, and calcium varied from 1298 to 13,855 ppm, indicating the soil was quite calcareous in places. In terms of agricultural fertility (Cornell Cooperative Extension 1990) the soil was low or very low in phosphorus and potassium (P: undetectable to 0.6 ppm, K: 18-61 ppm) while magnesium levels were high to very high (Mg: 188-368 ppm).

The vegetation was dominated by herbaceous species generally less than 25 cm in height. A few patches of bare ground, several meters across, were present but overall the ground was well vegetated. Woody species were sparse and generally restricted to the banks of the watercourse. The species richness of the vegetation of the Radio Lab field was quite high, with 69 vascular plant species being recorded by F. R. Wesley and the author in August 1987. The nomenclature of species identified during my site surveys follows Mitchell (1986) throughout the thesis. Relatively abundant species included *Solidago nemoralis*, *Aster pilosus* var. *pringlei*, *Panicum acuminatum*, *Daucus carota*, *Fragaria virginiana* and *Potentilla simplex*. In wetter patches, sedges were prominent, for example *Carex flava*, *C. folliculata* and *C. vulpinoidea*. A variety of woody species occurred, including *Viburnum recognitum*, *Cornus foemina* subsp. *racemosa*, *Salix discolor*, *S. bebbiana*, and *S. humilis*.

The land use history of the site had been one of farming followed by disturbance during the construction of the research facilities. Aerial photographs taken in 1938 and 1954 show the site as open farmland. (Photographs were supplied by CLEARs, the Cornell Laboratory for Environmental Applications of Remote Sensing.). In the 1960's it was used for space science research, which entailed levelling the field with a bulldozer so that a network of large antennae could be laid out. The site was fenced for safety reasons and mown about once a year. The antennae were removed in

1972 (G. StaSavage and P. Mosher, Cornell University, pers. comms.). The appearance of the site in 1986 matched well with this history of events. The patches of bare ground and lack of an organic horizon in places did suggest that topsoil had been removed in the past. Indeed, the bank, which continued along the eastern and southern boundaries of the field, may have been partly composed of bulldozed topsoil. *G. crinita* apparently had occurred nearby or on the site around the time of the disturbance as one local naturalist knew of its presence there since the late 1960's (R. B. Jones, pers. comm.). During my study, the population of *G. crinita* numbered in the thousands.

The Natural Area

The Fringed Gentian Natural Area was situated about 0.5 km away from the Radio Lab site and was also at 339 m above sea level. Again the topography was almost level. A small stream marked the northern boundary of the Area and a shallow ditch ran along the edge of the road parallel with the eastern boundary.

Soil parent material was glacial till and the soil types mapped for the site were predominantly poorly drained silty loams on shallow slopes. Soil types recorded in the 1960's were Langford channery silt loam (2-8% slopes), Erie-Ellery channery silt loams (0-3% slopes), Ilion silty clay loam (0-2% slopes), and Ellery, Chippewa and Alden soils (0-8% slopes) (USDA 1965). These types correspond to Fragiagquepts, Fragiochrepts, and Haplaquepts using more recent terminology (USDA 1971, 1973). The soil was generally at least 10 cm in depth over rock or hardpan. It was not stony and often had dark staining from organic material to a depth of at least to 10 cm. Soil samples taken for experiments described in Chapter 3 indicated that the Area had a lower range of pH and calcium levels than the Radio Lab field. Calcium levels recorded were around 929–2535 ppm and pH 5.3–6.2. Phosphorus was again very low (not detectable to 1 ppm) and potassium very low to medium (46–158 ppm). High to very high magnesium levels were recorded (118–313 ppm).

The vegetation of the Natural Area was composed mainly of woody shrubs some 3-4 m in height. The principal species were *Viburnum recognitum* and *Cornus foemina* subsp. *racemosa*. A few taller woody species overtopped the shrub canopy, for instance *Pinus strobus* and *Acer rubrum*. The herbaceous layer below the shrubs varied from thin to almost complete cover in places and included species such as *Rhus toxicodendron*, *Prunella vulgaris*, and *Fragaria virginiana*.

Two clearings were made in the scrub by Cornell Plantations staff in 1977, and were cut again in 1984. Here the vegetation was dominated by tall herbs and low woody plants about 1 m in height. There was no open bare ground but herbaceous cover below dense shrubs was thin to non-existent. The principal species present were *Cornus foemina* subsp. *racemosa*, *Viburnum recognitum*, *Solidago canadensis*, *S. rugosa*, *Euthamia graminifolia*, *Aster umbellatus*, and *A. novae-angliae*.

Between the eastern edge of the scrub and a road running north-south was an open roadside. The soil here was generally only 5-10 cm in depth above rocks or hardpan. It was rather stony and showed little evidence of an organic layer. The pH recorded for an aggregate soil sample was higher than within the Natural Area (pH 7.4) while calcium levels were somewhat similar (2017 ppm). Phosphorus was undetectable while potassium was very low (28 ppm) and magnesium very high (227 ppm). Short herbaceous vegetation less than 25 cm in height predominated along the roadside, and species present included *Aster pilosus* var. *pringlei*, *Daucus carota*, *Aster novae-angliae*, *Euthamia graminifolia*, *Fragaria virginiana*, *Juncus tenuis*, *Melilotus alba* and *Solidago nemoralis*. Bare and stony ground occurred in patches particularly towards the road but much of the roadside was well vegetated.

Aerial photographs taken in 1938 and 1954 show the Natural Area and its surroundings as a series of open fields bordered by hedges. Subsequent photographs taken in 1965, 1968 and 1980 indicate that woody plants increasingly spread into the fields. By 1985 the Area was largely covered with

scrub (pers. obs.). The roadside was mown by the highway authority, most recently in August 1986, and therefore remained open. Cornell Plantations staff mowed the roadside in 1990. The soil along the roadside had been disturbed in the past by some kind of road maintenance activity (D. McIlroy, local naturalist, pers. comm.). *G. crinita* was recorded from the Natural Area at least since the early 1960's (Dr. W. Dress, Cornell University; pers. comm.) when hundreds and perhaps even thousands of plants may have been present (Dr. W. Dress and B. King, Cornell University; pers. comms.). By the late 1980's few plants survived in the Natural Area but several hundred could be found along the roadside (pers. obs.).

Description of the Letchworth study site

The other site where detailed observations were made was situated in Letchworth State Park (latitude 42° 40' N, longitude 78° 0' W) about 160 km west of Ithaca (Fig. 2.1). It provided a contrast to the old field sites near Ithaca because it appeared to be an example of a natural habitat capable of supporting a *G. crinita* population. The *G. crinita* population studied was located on a northwest-facing landslip at an altitude of 330 m, above a deep gorge carved by the Genesee River. The landslip, which was one of several in the Park, occurred in glacial material overlying rocks of Devonian age, into which the gorge has been cut by post-glacial river erosion (Muller et al. 1988). Sandy and gravelly material in the upper morainic layers of the glacial deposits was underlain by silty lake sediments which behaved like impermeable clay. They acted as a barrier to water movement and continual slumping of saturated earth resulted (Dr. R. Young, Department of Geological Sciences, SUNY, Geneseo; pers. comm.). Hall (1843) gave a vivid description of the slide: "The whole surface for half a mile is saturated with water and springs gush out at every step." The landslip was still unstable in the 1980's, and small cracks and slumps occurred continuously during the project. It was observed that in periods of heavy rain, overland flow was established within minutes and water almost immediately began welling out of seepage areas.

The topography of the slide was quite variable. It was dissected by gullies which were steep sided in places, and swampy patches occupied flatter terraces between slopes. On some slopes, slumped material gave a 'rolled-carpet' appearance to the ground surface. Detailed study of the *G. crinita* population was confined to one part of the slide where four parallel transects 10 m by 40 cm were laid out parallel to the direction of the slope. The transects were bordered on one side by a gully of between about 20 cm to 1.5 m in depth. Slope angle, measured using a clinometer, was 25° and the slope itself was relatively stable. However erosion did occur during and immediately after the study period. Part of the transect nearest the gully side had been lost by the time field work was completed in 1989. In May 1990, Dr. Pat Martin (from Monroe Community College) reported that the gully had deepened and widened over winter and that the lower sections of the two transects furthest from the gully had been covered with mud and stones eroded from the slope above.

Soil depth along the transects varied from 2 cm (over rocks) to more than 60 cm of unconsolidated material, and no organic horizon was present. Chemical analysis of an aggregate sample showed that pH and calcium were quite high (pH 8.2, Ca 11,287 ppm) while phosphorus and potassium levels were very low (P: 0.5 ppm, K: 35 ppm) and magnesium levels were high (178 ppm).

Wooded land fringed the slide on all sides except the edge above the river. Trees had colonized part of the upper slopes of the landslip while lower down patches of scrub occurred. Woody species present included *Alnus incana* subsp. *rugosa*, *Cornus foemina* subsp. *racemosa*, *Populus tremuloides* and *Fraxinus americana*. Tall herbaceous species predominated in some areas, for example there were stands of *Scirpus atrovirens* and *S. cyperinus*. Shorter herbs and carpets of bryophytes were found in patches around marly springs and were characterized by species such as *Equisetum variegatum* and *Parnassia palustris*. Some stretches of ground, particularly on steeper, crumbling slopes, lacked any vegetation cover.

The transects area had a scatter of shrubs, particularly *Alnus incana* subsp. *rugosa* and *Salix rigida* which reached around 3 m in height in places. Bare ground and short herbaceous vegetation predominated, in roughly equal proportions. *Equisetum variegatum* was abundant in damp seepage areas. Other species present included *Solidago nemoralis*, *Melilotus alba*, *Leucanthemum vulgare* and *Daucus carota*, as well as *G. crinita*. Bryophytes from the transects have been collected and identified by Dr. Pat Martin. She found *Dicranella varia* (Hedw.) Schimp., *Preissia quadrata* (Scop.) Nees and a *Barbula* species, possibly *B. fallax* (Hedw.). All three species are characteristic of wet calcareous substrates, and the first two are typical of open, disturbed localities (Schuster 1949).

The landslide had been in existence for over 100 years. It was crossed in the nineteenth century by the Genesee Valley Canal, which was begun in 1836, completed in 1862, and closed in 1878 (Letchworth State Park information). Stone (1840) described the canal construction and how "great difficulties have been experienced from the extensive slides of the shelving hillside... These slides were in progress while I was there..." Hall (1843) gave a detailed description of the deposits exposed by the canal excavation and suggested that the area had long been unstable, although clearly the canal excavation had caused huge slides.

The canal was replaced by a railroad but that too closed (in the 1950's), at least in part because of the continual movement of material which constantly interrupted train travel (Letchworth State Park information). The landslip continued to be active after the closure of the railroad (T. Cook, local historian; D. Bassett, Naturalist for Letchworth State Park; pers. comms.). There was more movement in some years than others, as was found on a small scale in the transect area. Large scale landslip activity may have been related to wet weather in the preceding months, for instance in 1978 and 1988 landslips were active throughout the Park after very wet periods (D. Bassett, pers. comm.). Douglas Bassett recorded a population of *G. crinita* numbering thousands on the study site in the early 1980's though no earlier information about the presence of the plants exists. During my study the population continued to number in the thousands.

Climate and weather of the study sites

Across the western and central part of New York State where the study sites are located (Fig. 2.1), the climate is characterized by warm summers and long cold winters. In Tompkins County average daily maximum temperatures can reach around 80°F (27°C) in summer and temperatures of 90°F (32°C) or higher occur several days each year (USDA 1965). Average daily minimum temperatures can be below freezing from November to March (USDA 1965). Mean annual precipitation is 30-40 inches (76-102 cm) and mean total precipitation in the growing season (defined as May 1 to September 30) is 15-18 inches (38-46 cm) (Cline 1955).

During my field work, which extended from late 1986 to early 1990, an unusually dry period of about 6 weeks occurred from late May to early July 1988 in the northeastern U.S.A. (Knapp & Eggleston 1989). The study sites were in a region that had less than 30% of the precipitation normal for this time of year (based on the 30 year period 1951-1980). The summer was also unusually warm, particularly the period from mid-July to mid-August when 19 days had a temperature which exceeded 90°F (32°C) at Ithaca. Five days is the average number for this period, based on the years 1951-1980 (Knapp & Eggleston 1989).

The weekly rainfall amounts for stations at Ithaca and Portageville, which is about 2 km from the Letchworth site, are shown in Figures 2.6 and 2.7. The graphs reveal that both sites suffered a similar dry period in 1988. For a period of 5-6 weeks, 1 cm or less of rainfall per week was recorded. This was the longest dry period during the study and appeared to have the greatest effect on *G. crinita*. Other shorter dry periods of 1-3 weeks occurred in April each year, before the main flush of *G. crinita* seedling emergence, and also stretches of 1-2 weeks in July and August 1989 after

relatively high rainfall in May and June that year. The impact of the 1988 drought is discussed further in Chapter 5.

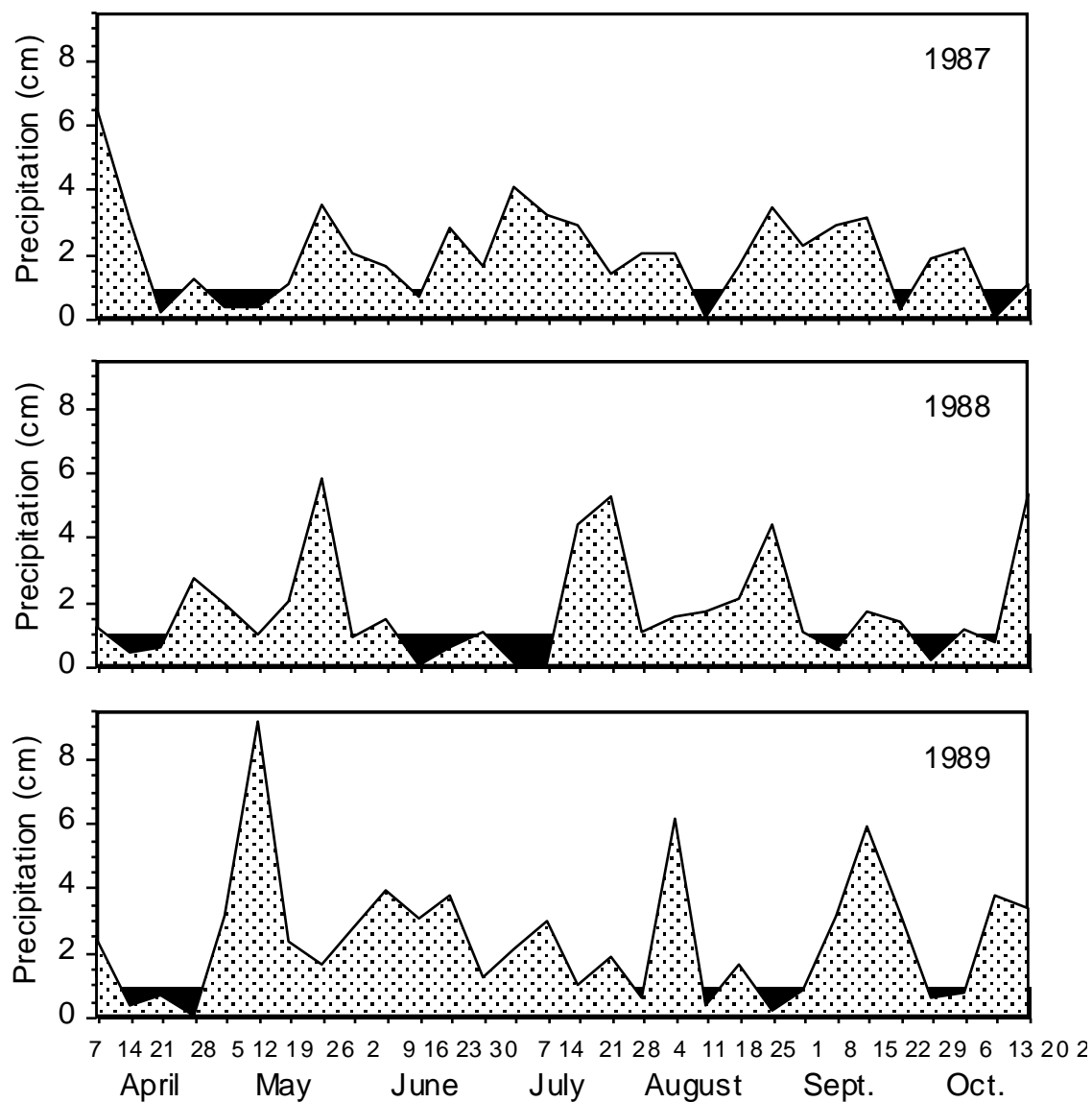


Fig. 2.6. Weekly rainfall recorded at the Ithaca weather station (5.3 km from the Radio Lab site) from April 1 through October, in the years 1987 to 1989 (from daily data, NOAA 1987-89). Black area (arbitrarily at 1 cm per week) highlights the dry periods.

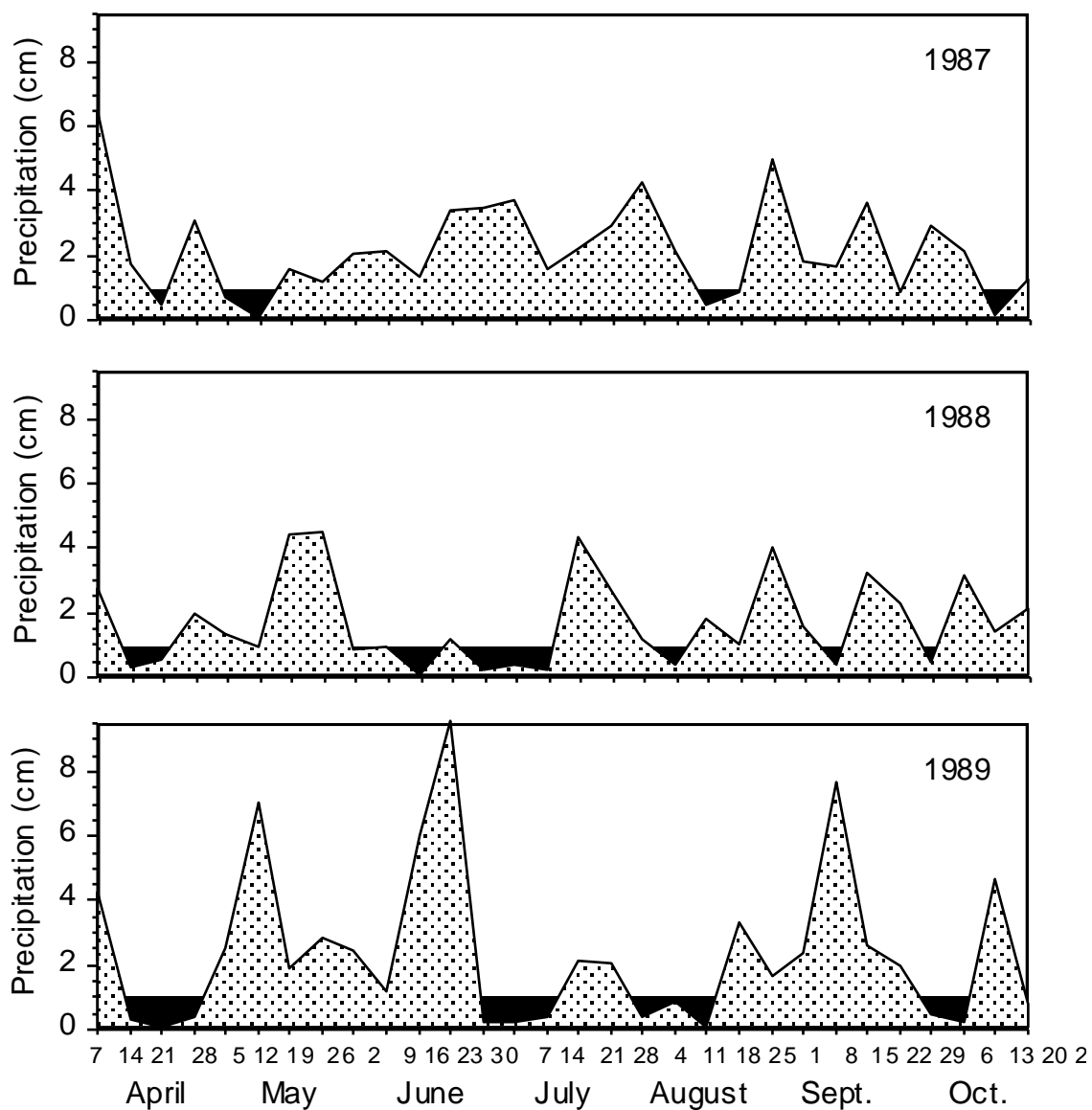


Fig. 2.7. Weekly rainfall recorded at the Portageville weather station (within 2 km of the Letchworth study site) from April 1 through October, in the years 1987 to 1989 (from daily data, NOAA 1987-89). Black area (arbitrarily at 1 cm per week) highlights the dry periods.

CHAPTER 3

PERSISTENCE, REGENERATION AND COLONIZATION BY *Gentianopsis crinita* IN A CHANGING LANDSCAPE

INTRODUCTION

Common biennials successfully occupy open habitats that are found in landscapes that are changing over time through the process of succession. Common biennials often occur, for example, in old fields in the forest regions of eastern North America (Holt 1972, Gross & Werner 1982, Goldberg 1987). Populations of common biennials may persist for a considerable length of time in open habitats before forest cover develops (Bard 1952, Pickett 1982). In grasslands and old fields they may occur in local patches of bare ground or in more or less closed swards of herbaceous vegetation (Grubb 1976, Gross 1980, Gross & Werner 1982, Thompson 1984, Goldberg 1987). Suitable habitats are available only intermittently in a forested landscape. For example, gaps in the forest made by treefalls are present only occasionally in time and space while relatively permanent open habitats such as cliffs or eroding river banks are usually sparsely distributed. However biennials are successful at colonizing these intermittently available open habitats (Grubb 1976, Hart 1977, Silvertown 1983, 1986). They can have efficient seed dispersal in space or long-lived buried seeds (Grubb 1976, Harper 1977, Gross & Werner 1982, de Jong et al. 1987, Grime et al. 1988).

Three hypotheses can be derived from these generalizations about biennials to focus the investigation of *G. crinita*'s relative scarcity. The hypotheses, which are outlined below, are not mutually exclusive but refer to different aspects of the ecology of *G. crinita* in relation to its ability to survive in landscapes where the distribution of open habitats is patchy in space and time. *D. carota*, a common biennial, provided a direct comparison against which to assess *G. crinita*'s performance.

Hypothesis 1: Compared to *D. carota*, *G. crinita* may be limited to early stages of succession after the ground has been disturbed because it might be unable to tolerate much competition from herbaceous species or woody plants. Alternatively, *G. crinita* might only appear briefly in later stages of succession when a herbaceous sward has already developed, for instance if the microclimate is more equable. Norton (1925) and Abbey (1930) found that *G. crinita* plants survived best from seeds that had been sown among herbaceous vegetation, apparently in contrast to their performance in open bare ground. These alternatives were examined by carrying out field experiments to test the hypothesis that *G. crinita* is scarce because it can survive through only a short part of a successional change from bare ground to forest. The experiments are described in Section I of this chapter.

Hypothesis 2: Biennials have no means of vegetative reproduction and must rely on seeds and seedlings for regeneration. These are usually small in size compared to adult plants and the places where regeneration occurs have been termed "microsites" or "microhabitats" (Grubb et al. 1982, Gross & Werner 1982). Microhabitats can be, for example, little patches of bare ground or moss. In open habitats where existing populations of *D. carota* and *G. crinita* occur, *D. carota* may be able to regenerate in abundance because it can successfully colonize a range of widely available microhabitats. In contrast *G. crinita* may be able to regenerate only in a scarce microhabitat. Recording of the regeneration of *G. crinita* and *D. carota* in different microhabitats was carried out at the Radio Lab field and at Letchworth to test the hypothesis that *G. crinita* is restricted in abundance by a scarcity of suitable microhabitats for colonization and regeneration, within those successional habitats where it can survive. The findings are described in Section II of this chapter.

Hypothesis 3: In a forested landscape, open habitats suitable for biennials are distributed intermittently in time and/or space. The only way that biennials can spread to new localities or recolonize sites that once had populations is by seed dispersal. *G. crinita* seeds may not have long-term viability and therefore the species would be unable to recolonize an area from a buried seed

bank, while spatial dispersal may be limited in some way, for instance, seeds may not survive dispersal by water. Thus the third hypothesis is that *G. crinita* is rare because it has limited colonizing abilities due to its poor seed dispersal capabilities. Section III of this chapter describes how the hypothesis was tested by carrying out observations and experiments at the study sites near Ithaca or in the greenhouse at Cornell University.

SECTION I. PERSISTENCE OF *Gentianopsis crinita* IN SUCCESSIONAL HABITATS

Introduction

Two field experiments were carried out at the Fringed Gentian Natural Area over the period 1987 to 1989 to discover if *G. crinita* is scarce because it can survive through only a short part of a successional change from bare ground to forest. The Natural Area was a suitable place for the experiments as it had changed from open fields to scrub over the last 20 to 30 years (Chapter 2). During this time the *G. crinita* population had declined so that by the late 1980's only a few plants were present. In 1977 and 1984 attempts were made by Cornell Plantations staff to conserve the gentians by clearing scrub in two places, but without much success (Dr. Nancy Ostman, Cornell University; pers. comm. and pers. obs.). Cut material was removed from the clearings but management such as deliberate ground disturbance or regular mowing was not undertaken. In 1977 some unsuccessful attempts were made to burn the scrub (Dr. M. Richmond, Cornell University; pers. comm.).

One experiment was set up in the clearings and one in the uncut scrub in 1987. The treatments across the two experiments were designed to simulate a range of successional habitats by creating different intensities of disturbance and competition over a short time scale of two years. The conditions ranged from heavily disturbed ground in the clearings, where the vegetation was regularly mown, to undisturbed ground in the tall uncut scrub. It was assumed that the intensity of interspecific competition increased with the aboveground size of other plants, relative to the size of *D. carota* and *G. crinita*. Thus, for example, in the clearings where all herbaceous and woody plants were clipped, competition would be lower than in unmown plots. In turn, competition in these unmown plots in the clearings would be less than in plots under the tall scrub.

The responses of *G. crinita* and *D. carota* to the different treatments were measured by sowing seeds of the two species and recording life history characteristics such as seedling emergence, survival of vegetative plants, and reproductive output. Environmental and biotic factors, for example light levels, plant cover, and incidence of herbivory, were also recorded in order to obtain clues about the underlying reasons for any observed effects of ground disturbance or clipping of other plants.

The specific questions addressed by the experiments were:

1. Was disturbance necessary for seedling emergence?
2. Once seedlings emerged, did survival and reproduction only occur where there were low rather than high levels of interspecific competition from other plants?
3. Could the failure of previous conservation efforts at the Natural Area be attributed to 1. or 2.?

Materials and Methods

Experiment in the existing clearings: 1987-89

The experiment was set up in November 1987. At this time the vegetation in the clearings consisted mainly of tall herbs and low woody shrubs about 1 m high. The principal species were *Solidago canadensis*, *S. rugosa*, *Euthamia graminifolia*, *Aster umbellatus*, *A. nova-angliae*, *Cornus foemina* subsp. *racemosa* and *Viburnum recognitum*.

Experimental design, treatments, and measurements







Five treatments were applied to 15 plots in each of 5 blocks laid out in the two clearings, to provide differing degrees of disturbance and competition. Two blocks were located in the existing northern clearing and three in the southern clearing (see Fig. 3.1). The blocks were 5 m apart within each clearing. An example of the layout of the plots and treatments in a block is shown in Fig. 3.2. The plots were 40 cm by 40 cm square and 40 cm apart. Given the small size of *G. crinita* and *D. carota* plants (especially the seedlings of the two species), the plot size was chosen as a practical compromise between achieving discernible treatment effects and searching and monitoring each plot thoroughly without disturbing it.

Four initial treatments were randomly allocated to plots and applied in November 1987:

1. Heavy disturbance. Vegetation was clipped close to the ground (5 cm height), all loose litter and clippings were removed and the plot dug over to a depth of about 10 cm with a shovel. No roots were removed although many were severed by the shovel. The earth was then smoothed by hand that the surface was level bare ground. (3 plots per block)
2. Light disturbance. Vegetation was clipped to 5 cm height and loose litter and plant clippings removed. (3 plots per block)
3. Mowing. Vegetation was clipped to 5 cm and the clippings removed but the natural litter was left in place. (6 plots per block)
4. No treatment. These "control" plots were left untouched. (3 plots per block)

At intervals during 1988 and 1989, the vegetation in the plots given initial treatments 1-3 was clipped to about 5 cm in height and the clippings removed. Any stems of herbaceous or woody plants overhanging these plots were clipped back at the same time. The schedule of mowing dates is shown in Fig. 3.2. The regime meant that five treatments were in operation during the experiment: two types of initial ground disturbance where vegetation was subsequently mown more than once a year; two types of mown plots, one of which was clipped more frequently than the other; and one treatment where the ground was left undisturbed and the vegetation unmown. Mowing was done on census dates (given below) when life history characteristics of *G. crinita* and *D. carota* were being recorded.

In November 1987, immediately after the initial treatments had been applied to the plots, 300 seeds of *G. crinita* were sown in each of 5 plots per block, and 300 seeds of *D. carota* were sown in each plot of a separate set of 5 plots per block, as shown in Fig. 3.2. The seeds were sown as evenly as possible. Unseeded plots were included in the experiment to get a measure of the response of any native seeds already existing on the site. No seed-bearing individuals of either species occurred within or around the blocks. Species were randomly allocated to plots within blocks so that each species/treatment combination was represented.

- | | | | |
|---|---------------------------------------|---|---------------------------------|
|  | Blocks in existing clearings: 1987-89 |  | Existing clearings |
|  | Block in existing clearing: 1988-89 |  | Large plots cleared in 1987 |
|  | Blocks in scrub: 1987-89 |  | Transect for soil samples: 1987 |

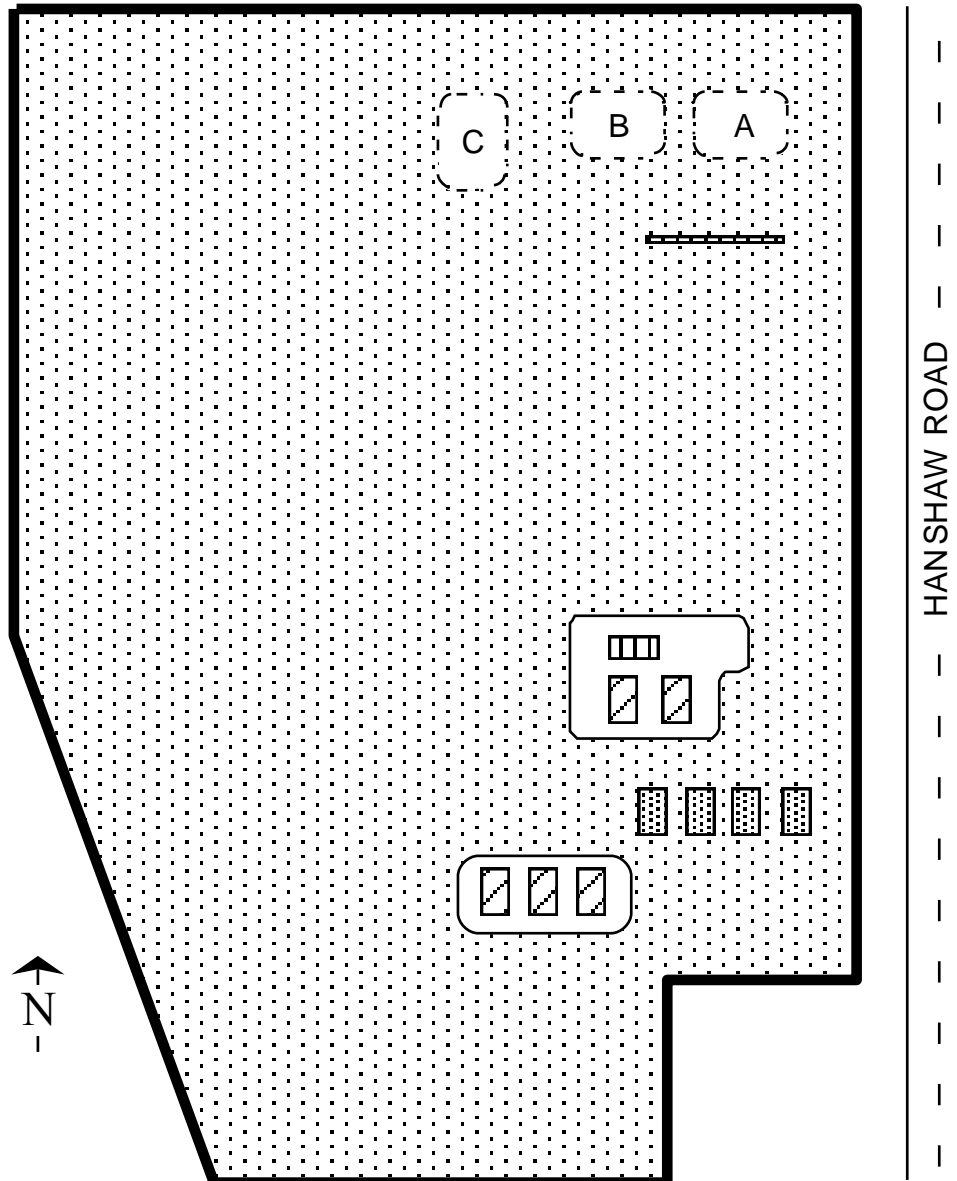
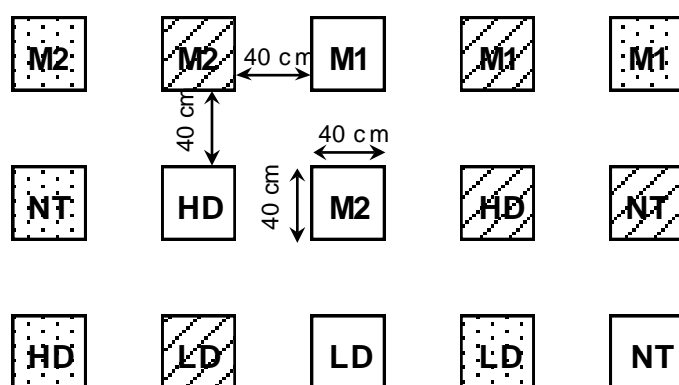


Fig. 3.1. Layout of the experiments in the Natural Area (not to scale). Blocks in the existing clearings and scrub were set up for experiments described in Section I, Chapter 3. Layout of treatments in 1987-89 blocks is shown in Figs. 3.2 and 3.3. Plots A-C were cleared and soil samples were taken along the transect for experiments described in Section III, Chapter 3.



a)

	300 <i>G. crinita</i> seeds sown, November 1987
	300 <i>D. carota</i> seeds sown, November 1987
	No seeds sown
HD = Initial heavy disturbance + mown > once a year	
LD = Initial light disturbance + mown > once a year	
M2 = Mown > once a year	
M1 = Mown once a year	
NT = No treatment	

b)

	Initial treatment	Subsequent treatments				
	1987	1988			1989	
	November	June	July	Sept.	June	July
HD	Heavy disturbance	mown	mown	mown	mown	mown
LD	Light disturbance	mown	mown	mown	mown	mown
M2	Mown	mown	mown	mown	mown	mown
M1	Mown	mown	-	-	mown	-
NT	No treatment	-	-	-	-	-

Fig. 3.2. Experiment in the existing clearings at the Natural Area in 1987-89.

- Example of random layout of treatments in a block.
- Schedule of treatments applied to plots through the period 1987-89. Note: there was little growth of vegetation between July and September in 1988 and 1989. No mowing was done in September 1989.

The seeds had been collected in the fall of 1987 from *G. crinita* and *D. carota* plants growing along the roadside adjacent to the Natural Area as there were too few plants present within the preserve to supply sufficient seed. The roadside supported the closest population of *G. crinita* to that in the preserve (Chapter 2) and the plants on the roadside probably formed part of a larger preserve population in the past. If significant ecotypic differentiation exists between *G. crinita* populations in separate sites, as has been found for other species (Turkington & Harper 1979, Waser & Price 1985), then the roadside population seems likely to be reasonably similar genetically to the population within the Natural Area. Responses to the treatments by the introduced plants should therefore be fairly similar, thus increasing the reliability of subsequent management recommendations aimed at conserving the population within the preserve.

Seedling emergence, survival and flowering of plants were followed for two years. In 1988, seedlings that emerged in the plots were censused in early June (3rd-11th), after the main flush of *G. crinita* emergence which generally occurs in late May. Each plant was mapped by placing a quadrat, divided into 100 4 x 4 cm squares, over the plot and recording the position of the plant on a grid map of each plot. Plants were marked with plastic-covered wire placed close to each plant. Censuses were repeated at approximately six-week intervals in late July (20th-26th), mid-September (10th-13th), and the end of October (24th to November 1st). In October, a random sample of 15 plants was selected from each plot and the diameter of rosettes measured. If fewer than 15 plants were present in a plot, then all plants were measured.

An unusual period of severe drought began in May 1988 (see Chapter 2), and the entire experiment was judged to be at risk. To ensure that information was obtained on the role of competition under more normal weather conditions, the plots were watered on four occasions with 4 L of tap water (21st June, 28th June, 7th July and 16th August). The water was applied as evenly as possible by using watering cans fitted with spray nozzles. The amount of water supplied to the plot was equivalent to 2.5 cm of rainfall on each occasion. The amount was based on an estimate of rainfall under more normal conditions of around 2.5 cm every week or 10 days. For two-thirds of the period from 29th May to 16th August 1988, the watering resulted in the water supply to the plots being between the cumulative rainfall values for 1987 and 1989, and within 2.5 cm of these values for over 95% of the time. Although the amounts supplied were similar to rainfall in more normal seasons, evaporation would probably have been somewhat greater, because the 1988 summer temperatures were unusually warm (Knapp & Eggleston 1989). The actual impact of the drought on *G. crinita* was not ignored in my study as its effects were the subject of observations made at the Radio Lab field and described in Chapter 5.

In 1989, censuses were carried out in May (9th-15th), mid-June for new seedlings only (14th-23rd), late July (23rd to 2nd August), mid-September (10th-14th), and the end of October (23rd-27th). Stems of all of the second-year *G. crinita* and some of the second-year *D. carota* had begun to elongate by May 1989. These "bolting" stems were not clipped when the rest of the plants in a plot were mown according to the schedule shown in Fig. 3.2. Numbers of flowers (*G. crinita*) or umbels (*D. carota*) on individual plants that had bolted were recorded along with survival of all second-year plants.

Additional experiment in one of the existing clearings: 1988-89

Rapid regrowth of vegetation over the bare ground of the disturbed plots was noted during May and June 1988. If the seedlings of one species had emerged earlier than those of the other species, the difference in timing of seedling emergence could have been important in determining the relative response of the two species to this temporary reduction in competition from other plants in spring and early summer. Therefore in the fall of 1988 an additional set of heavy disturbance plots was prepared in one of the existing clearings (Fig. 3.1) to get a better estimate of the time when seedlings of the two species emerged relative to each other. Six 1 m by 1 m plots were clipped and dug over, and 50 seeds of either *G. crinita* or *D. carota* were sown in the central 20 by 20 cm part of each plot. The plots were clipped on 23rd May and 14th June 1989. Emergence was recorded every 2 to 3 days beginning 21st April, before any seedlings emerged, until 8th July. The plots were checked weekly during the remainder of July and biweekly from August to November.

Experiment in the scrub: 1987-89

To investigate the response of the two species to conditions in later successional habitats where woody species predominate, a field experiment was laid out in November 1987 in the tall scrub between the two existing clearings (Fig. 3.1). The scrub was 3 to 4 m in height and the canopy was virtually closed. The principal species were *Viburnum recognitum* and *Cornus foemina* subsp.

racemosa. Four blocks were laid out along a transect beginning 10 meters from the roadside edge of the scrub. The blocks were 5 m apart, and each had six 40 cm by 40 cm plots, 40 cm apart. The layout is shown in Fig. 3.3. Two treatments were applied in each block: loose litter was removed ('disturbance') or the plots were left undisturbed ('no treatment'). Three hundred seeds of each species were spread separately in two plots per block while two plots were left unseeded (Fig. 3.3). Species/treatment combinations were randomly allocated to plots. Seedling emergence, size and survival of plants were recorded in the same way and during the same periods as for the experiment in the clearings. The plots were watered with 4 liters per plot at the same times in 1988 as the plots in the clearings. In October 1988, litter was again removed from the plots which had been cleared in fall 1987 to see if differences in seedling emergence occurred between treatments in the second year after planting.

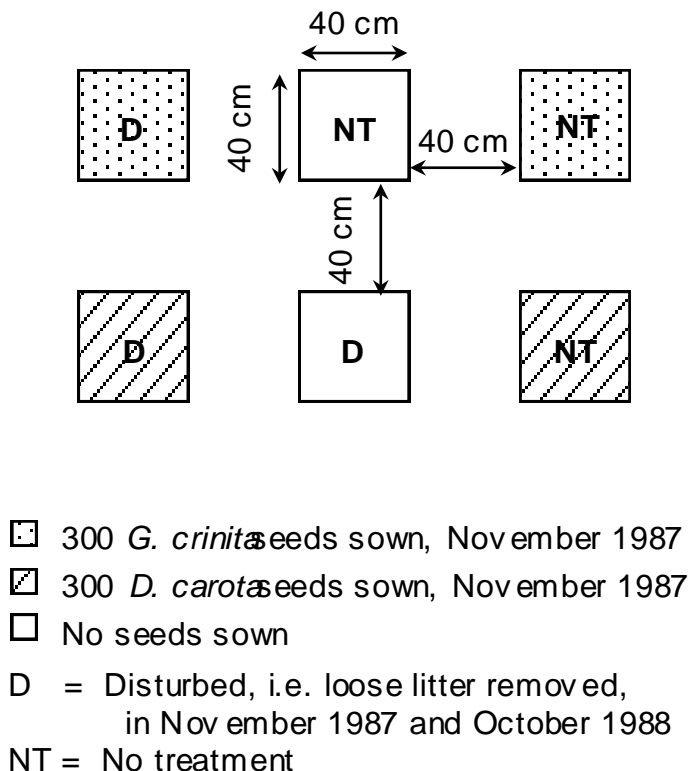


Fig. 3.3. Experiment in the scrub at the Natural Area: 1987-89. Example of random layout of treatments in a block.

Environmental measures and herbivory

To identify possible causes of differences or similarities in the response of the two species to the treatments, various measures were taken of abiotic and biotic factors. Percent plant cover of herbaceous and woody plants less than 1 m in height was recorded in June and July 1988 and June 1989, during the census periods and before plots were clipped. A 40 by 40 cm quadrat divided up into 100 4 x 4 cm squares was used to estimate cover by eye. Light measurements were made on 23rd July 1989 with a LiCor light meter in units of mEinstein/m²sec. The average of three randomly located readings was taken at both 5 cm and 15 cm height above the ground in each plot. The readings were expressed as a percent of the light reading taken 1.5 m above the plot immediately after the readings were made within the plot. Readings in the scrub were made in the same way but expressed as a percent of the average of two readings taken in the open before and after the readings were made in the scrub.

Relative soil moisture tension was measured in centibars of soil suction in each plot using a Model 2900F Soil Moisture probe on 15th June 1988 (before any watering was done) and on 29th July 1988. Each reading was made at 5 cm depth one minute after insertion of the probe into the soil. The average of two readings was taken from the northwest and southeast corners of each plot.

Soil chemistry and organic matter were determined from samples collected in November 1989. A 2 cm diameter soil corer was used to extract five subsamples from the upper 10 cm of the soil in each plot that had been seeded with *G. crinita*. The subsamples were well mixed and a composite sample given to the Cornell Nutrient Analysis Laboratories for analysis. The soil factors analyzed were pH, loss on ignition (an index of organic matter), extractable phosphorus, potassium, magnesium, calcium, iron, aluminum, manganese, and zinc. Soil pH was determined from a 1:1 (by volume) soil: water suspension. Loss on ignition was determined by drying the soil at 50° C for one hour, then igniting it at about 500° C for two hours. Nutrients were extracted with 10% sodium acetate in 3% acetic acid buffered to pH 4.8, using a 1:5 (by volume) soil: solution ratio. Potassium, magnesium, calcium, manganese, iron, aluminum and zinc were determined by atomic absorption. Phosphorus was determined colorimetrically by stannous chloride reduction.

The incidence of herbivory was estimated by the presence of obvious chewing damage on rosette leaves in October 1988. The causes of damage were not known. Invertebrates probably damaged *G. crinita* rosettes and some *D. carota* rosettes but larger *D. carota* rosettes may also have been damaged by mammals. The estimate of damage did not include missing plants that may have been totally eaten during the field season.

Data analysis

Data were analyzed using the SAS program Proc GLM (SAS Institute 1985) to produce ANOVA tables. Treatment differences were analyzed within each species and between species. A few comparisons using non-parametric tests were made between the results of the experiment in the clearings and the experiment in the scrub.

For the results of the experiment in the clearings, weighted analyses were done in addition to unweighted analyses in cases where numbers of plants per plot within treatments differed widely, since in an unweighted analysis, data from plots with very few plants affect the overall average as much as plots with larger sample sizes, which might be more reliable. However, the weighted analysis, which relies more heavily on plots with many plants, may be biased if there are density effects. Unweighted and weighted analyses were done to see if the results were affected. The results of the two types of analysis were similar. The unweighted analyses were more conservative compared to the weighted analyses, which picked up a few more of the differences between treatments. These additional results are given below, along with significant results of the unweighted analyses.

Where necessary, transformations of data were used to stabilize variances. The means and their associated standard errors which are quoted in the Results Section have been back transformed where appropriate. For the experiment in the clearings, a set of orthogonal contrasts of means was used to analyze the differences between treatments and, in addition, Dunnett's one-sided test of treatments against a control (i.e., 'no treatment') was made (Chew 1977).

Results

Experiment in the existing clearings

Seedling emergence

The average proportion of *G. crinita* seeds that germinated and emerged per treatment in 1988 did not exceed 26%, which was similar to the maximum per treatment for *D. carota* (less than 29%; Table 3.1). Lower proportions of seedlings of both species emerged in the undisturbed plots with high levels of competition ('no treatment'), but for *G. crinita* no significant differences were found (Table 3.2). However, significantly more *D. carota* seedlings emerged in the lightly disturbed plots with low levels of competition compared to the 'no treatment' plots (Table 3.2). Actual percent emergence in individual plots within one treatment varied widely in some cases; for example, 7.3 - 38.7% and 10.7 - 32.0% in the heavy disturbance treatment for *G. crinita* and *D. carota* respectively. No differences in percent emergence across treatments were found between the two species ($p = .85$). Emergence rates are likely to be minimum estimates because some plants probably emerged and died between census periods.

Very few seedlings emerged from the 25 unseeded plots. One *G. crinita* seedling and 24 *D. carota* seedlings were recorded during the first year. In the second year only one *G. crinita* and two *D. carota* seedlings were recorded. The low numbers of 'native' seeds that emerged and the lack of any seeding plants of either species in the blocks in the fall of 1988 suggest that the numbers emerging in seeded plots in 1989 can be regarded as a reasonable estimate of the percent out of 300 that emerged and were counted at the census dates in the second year after planting.

Both species showed low percent emergence in 1989 with maxima around 2%. However, *G. crinita* did respond differently to the treatments. Average percent emergence was 2.0% in the heavy disturbance treatment, significantly more than in light disturbance or 'no treatment' plots (Table 3.2). Percent emergence was $\leq 0.3\%$ in these latter treatments and the two other treatments. Emergence of *D. carota* did not differ between treatments. In the factorial analyses of species difference, the treatment and species terms interacted so that the main effect of species across treatments could not be assessed.

Table 3.1. Experiment in the existing clearings at the Natural Area: mean responses of *G. crinita* and *D. carota* (5 replicate 40 cm x 40 cm plots per treatment/species combination). Since means are back-transformed, and may have asymmetric back-transformed standard errors, the back-transformed range of ± 1 s.e. is given (the difference between the mean plus 1 standard error and the mean minus 1 standard error).

	Heavy disturbance		Light disturbance		Mown more than once		Mown once		No treatment	
	Mean	range ±1 s.e.	Mean	range ±1 s.e.	Mean	range ±1 s.e.	Mean	range ±1 s.e.	Mean	range ± 1 s.e.
<u>% Emergence 1988 *</u>										
<i>G. crinita</i>	23.0	13.4	25.6	10.4	16.6	8.9	22.2	8.3	14.5	8.4
<i>D. carota</i>	21.3	6.6	28.2	9.0	22.2	3.3	18.9	10.9	13.8	4.1
<u>% Emergence 1989 *</u>										
<i>G. crinita</i>	2.0	2.8	0.1	0.4	0.3	0.4	0.2	0.5	0.1	0.2
<i>D. carota</i>	1.7	2.1	2.5	1.3	1.7	0.5	1.7	0.5	2.0	1.1
<u>% Establishment *</u>										
<i>G. crinita</i>	61.4	5.8	57.4	17.7	69.0	7.4	53.5	27.6	51.5	15.9
<i>D. carota</i>	83.3	7.5	85.5	9.8	84.1	5.9	91.8	8.8	72.6	17.7
<u>Size October 1988 [†]</u> (rosette diameter in mm)										
<i>G. crinita</i>	24.5	6.4	22.7	5.4	30.0	7.2	24.3	5.4	23.1	5.6
<i>D. carota</i>	172.4	51.9	97.5	53.3	130.3	15.7	135.6	27.2	66.7	24.1
<u>% Survival over winter *</u>										
<i>G. crinita</i>	72.6	16.0	70.8	7.3	69.0	7.4	54.5	25.6	47.5	27.6
<i>D. carota</i>	82.6	9.1	78.6	21.1	83.3	14.8	81.0	20.2	69.9	12.8
<u>% Survival in 1989 *</u>										
<i>G. crinita</i>	68.0	29.3	56.4	21.6	84.8	14.3	41.5	40.2	28.2	31.7
<i>D. carota</i>	64.3	17.2	70.8	14.5	68.0	14.9	78.6	13.1	60.4	9.8
<u>% Survival over 2 years *</u>										
<i>G. crinita</i>	26.4	10.6	20.5	8.1	38.6	5.8	17.4	22.4	6.6	9.9
<i>D. carota</i>	43.5	17.8	48.5	27.6	46.5	15.9	58.4	27.2	30.0	14.6
<u>Flowers per plot [‡]</u>										
<i>G. crinita</i>	26.9	16.8	21.3	10.2	28.2	21.9	17.1	31.2	2.2	2.6
<i>D. carota</i>	11.8	4.4	2.5	3.6	3.2	4.2	0.6	1.0	0	0

Data transformed by: * = arcsine square roots; [†] = natural logarithms; [‡] = square roots.

Table 3.2. Experiment in the existing clearings at the Natural Area. Analysis of responses of *Gentianopsis crinita* and *Daucus carota* to the different treatments. Only p values < .05 are shown, for differences among and between treatments from ANOVA. The α -level for Dunnett's test, comparing each treatment with the controls, is 0.05 ("+" = $p < .05$). Unweighted analysis: plain type. Additional significant results from weighted analysis: [in brackets].

	<u>% Emergence</u>		Estab- lishment	Size October	<u>% Survival</u>			Flowers per plot
	1988	1989	1988	1988	over winter	in 1989	over 2 years	
<i>Gentianopsis crinita</i>								
Difference among treatments	-	.005	-	-	[.007]	-	.045	-
No treatment vs. other treatments	-	-	-	-	-	[.03]	.01	.007
Heavy vs. Light disturbance	-	.001	-	-	-	-	-	-
Mown once vs. More than once	-	-	[.048]	-	[.02]	[.0002]	[.01]	-
Mown vs. Disturbed	-	-	-	-	[.008]	-	-	-
Dunnett's test, No treatment versus:								
Heavy disturbance	-	+	-	-	-	-	+	+
Light disturbance	-	-	-	-	[+]	-	-	-
Mown > once	-	-	[+]	-	-	+	+	+
Mown once	-	-	-	-	-	-	-	-
<i>Daucus carota</i>								
Difference among treatments	-	-	-	.005	-	-	-	.0003
No treatment vs. other treatments	.047	-	.02	.001	-	-	-	.0008
Heavy vs. Light disturbance	-	-	-	.02	-	-	-	.005
Mown once vs. More than once	-	-	-	-	-	-	-	-
Mown vs. Disturbed	-	-	-	-	-	-	-	.008
Dunnett's test, No treatment versus:								
Heavy disturbance	-	-	-	+	-	-	-	+
Light disturbance	+	-	[+]	-	-	-	[+]	+
Mown > once	-	-	-	+	-	-	-	+
Mown once	-	-	+	+	-	-	+	-

Timing of seedling emergence

D. carota seedlings emerged earlier than *G. crinita* seedlings during spring 1989 in the additional experiment, which was set up in one of the clearings in fall 1988. Nearly 50% of the *D. carota* seedlings that emerged between 27th April and 8th July were recorded as present before 13th May 1989. In contrast only 2% of *G. crinita* seedlings had appeared by that date (Fig. 3.4).

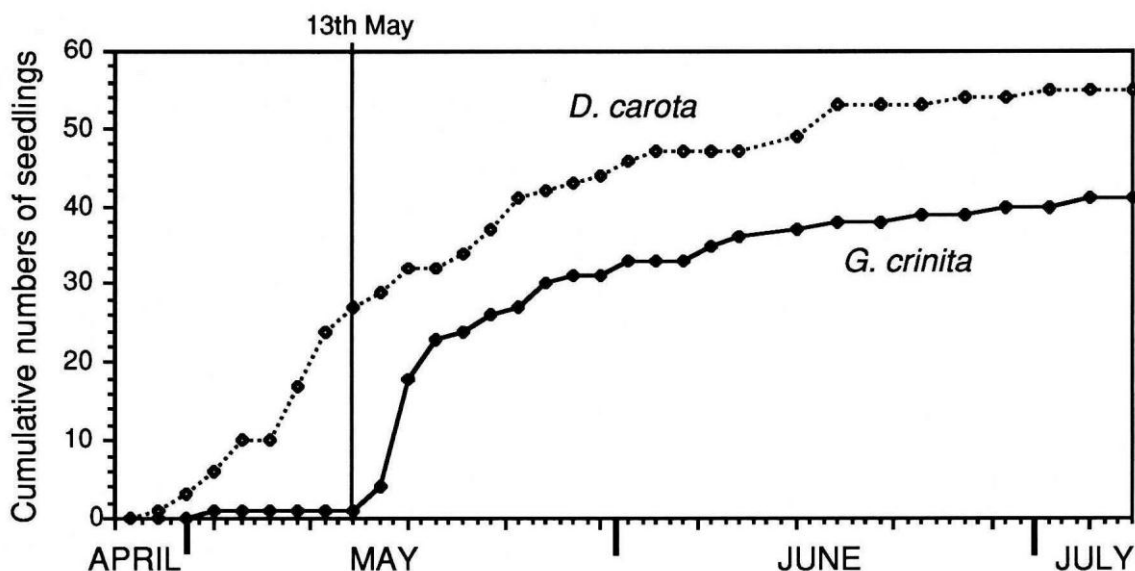


Fig. 3.4. Timing of emergence of *D. carota* and *G. crinita* seedlings in the 1988-89 block of 'heavy disturbance' treatment plots in one of the Natural Area clearings (shown in Fig. 3.1). The graph shows cumulative numbers of seedlings emerging between 27 April 1989 and 8 July 1989. A total of 150 seeds of each species were sown in fall 1988. By 13th May 1989, 49% of the total number of *D. carota* seedlings that emerged between 27 April and 8th July 1989 had appeared, while only 2% of *G. crinita* seedlings had emerged by 13th May. No seedlings appeared before 27th April 1987.

Establishment and size in 1988

G. crinita's establishment success in 1988 (percent of numbers present in October compared to the total that emerged during the year) was over 50% on average (Table 3.1) and was not different between treatments in the unweighted analysis (Table 3.2). *D. carota*'s establishment success was over 70% on average (Table 3.1). There was a different response in the untreated plots compared to the average of the other treatments, but only the 'mown once' plots had significantly greater establishment than the 'no treatment' plots (Dunnett's test) in the unweighted analysis (Tables 3.1, 3.2). However, numbers of seedlings emerging per plot varied quite widely within each treatment for both species, especially *G. crinita*. Therefore a weighted analysis was done by multiplying the establishment percent by the total number that emerged in each plot.

The weighted analysis detected slightly greater establishment of *G. crinita* in plots mown more than once compared to plots mown only once a year (Table 3.2). Dunnett's test indicated that establishment was greater ($p < .05$) in plots mown more than once a year compared to 'no treatment' plots.

For *D. carota*, the weighted analysis indicated that there was significantly lower establishment in 'no treatment' plots compared with the average of establishment in the other treatments (Table 3.2). In addition Dunnett's test showed that 'light disturbance' and 'mown once' had greater establishment than the 'no treatment' plots ($p < .05$).

It should be noted that the establishment percents found for both species in this experiment, and in the experiment in the scrub (discussed later), are slight overestimates as those seedlings emerging and dying between censuses are not included.

At the end of 1988 there was no difference in size (rosette diameter) of *G. crinita* plants between treatments. In contrast, *D. carota* plants grew larger where competition was reduced (Table 3.2). The size data for both species were also used in an analysis of overwinter survival (see below). The size measure used in the experiments, i.e. rosette diameter, is not comparable between the two species as they have different leaf morphologies (Figs. 2.4, 2.5). No harvesting was done, so no objective measure of biomass was obtained.

Overwinter survival

No difference between treatments in overwinter survival from October 1988 to early May 1989 was detected for either species, in the unweighted analysis (Tables 3.1, 3.2), although there was a trend towards greater survival of *G. crinita* plants where competition was reduced (Table 3.1). Weighted analysis, using the number of plants present in each plot in October 1988 as weights, also indicated no difference for *D. carota*. The results for *G. crinita* supported the trend seen in the unweighted analysis. There was significantly greater survival in disturbed compared to mown plots, in plots mown more than once a year compared to plots mown once a year, and in plots that had been lightly disturbed compared to 'no treatment' plots (Table 3.2).

The effect of size on ability to survive the winter was assessed for both species. The rosette diameter data for *G. crinita* in all plots were combined and a non-parametric test done to see if size in October 1988 was associated with survival until May 1989. The median size (27 mm) was used to divide the data into two groups. A χ^2 test of frequency of alive or dead plants in May 1989 in these two groups found that small plants were more likely to die over winter ($N = 350$, $p < .0001$). The median rosette size of *D. carota* was 140 mm, and as for *G. crinita*, small plants were more likely to die over winter ($N = 373$, $p < .005$).

Survival in 1989

G. crinita survived better in 1989 in plots where competition had been reduced by mowing more than once a year compared to survival in undisturbed plots, either mown once a year or unmown, according to the weighted analysis (Tables 3.1, 3.2). This analysis used numbers of plants present in May 1989 as weights. The survival of *D. carota* plants during 1989 did not differ between treatments (Table 3.2).

Overall survival during the experiment

Strictly speaking, the above analyses form part of one overall response by each species to the treatments. However there were no *a priori* reasons to suppose that survival at each stage would be positively correlated with survival in the other stages. In fact, weighted and unweighted analyses of *G. crinita*'s survival over two years, i.e. numbers present in October 1989 compared to total that emerged in 1988, confirm the suggestion given by the stage analyses of greater survival of the plants in the 'mown more than once' and 'heavy disturbance' treatments compared to the plants in the 'no treatment' plots. Average survival was about 3 to 6 times greater in those plots where competition had been reduced, even in plots mown only once a year, compared to undisturbed, 'no treatment'

plots with high levels of competition (Tables 3.1, 3.2). For *D. carota*, plants in the 'mown once' (unweighted and weighted analyses) and 'light disturbance' treatment (weighted analysis only) survived better than plants in 'no treatment' plots ($p < .05$), although the differences were less marked than those for the relative survival of *G. crinita* among treatments (Tables 3.1, 3.2).

When the two species were compared, *D. carota* had greater survival during all stages and overall ($p < .05$), with the exception of survival during 1989 when there was no difference.

Reproductive output

To measure the effect of the different treatments on reproductive output, the total number of flowers or umbels produced per plot was used. This seemed to be the most appropriate 'plot-level' measure of treatment effect, rather than mean number of flowers or umbels per plant.

No estimates of damage by herbivores to flowers or umbels were made. *D. carota* had suffered some herbivory by September 1989, and some *G. crinita* flowers had been nipped off by October. Deer were probably responsible for the damage in both cases. Damage to the 2 species was particularly noticeable in plots around the edges of the blocks in the southern clearing. Therefore, to assess treatment effects, rather than plot position effects, comparisons of flower and umbel numbers were made using late July figures for *D. carota* and mid-September figures for *G. crinita*. The July figures for *D. carota* may slightly underestimate umbel numbers compared to those that might have been present in September if no damage had occurred. However, records made at the Radio Lab site, which are described in detail in Chapter 4, showed that where little damage occurred, numbers of umbels were not very different over time. Between mid-August and mid-September 1989 there was less than 1% difference in umbel numbers while between mid-July and mid-September 1988 there was <15% difference.

In the clearings at the Natural Area, *D. carota* plants produced no umbels in the 'no treatment' plots, in contrast to *G. crinita*, which did flower (Table 3.1). *G. crinita* produced on average at least twice the number of flowers per plot compared to numbers of *D. carota* umbels per plot in the other 4 treatments (Table 3.1, $p = .0001$ for the comparison between species).

Total number of flowers per plot combines number of plants and their flower numbers. Given that most of the *G. crinita* plants which flowered had only one flower (75%), it is not surprising that the treatments with the best overall survival (i.e. 'heavy disturbance' and 'mown more than once') had significantly greater numbers of flowers than 'no treatment' plots (Table 3.2). Observations made at other sites suggest that *G. crinita* never lives longer than two years, so no further seed production would be likely from the 1988 cohort in future years.

However, *D. carota* is a "facultative" biennial, i.e. it can survive an indeterminate number of years as a vegetative rosette before it flowers (Kelly 1985). For example, the 'no treatment' plots produced no flowers even though the plants had survived for two years but the rosettes might have survived into 1990 and beyond. The appearance in the field of many flowering *D. carota* plants in the 'heavy disturbance' plots was striking, and was confirmed by the analysis of numbers of umbels per plot (Table 3.2). More umbels were produced in plots that had been disturbed then mown rather than just mown, and more umbels were produced in plots that had been heavily rather than lightly disturbed.

Environmental measures and herbivory in the existing clearings

Most of the other plant species present in the experimental area were perennials and they recovered quickly during 1988 after the disturbance treatments in the fall of 1987. In June 1988, disturbed plots had lower percent cover than mown plots, and heavily disturbed plots less cover than lightly disturbed plots (arcsine-transformed data, $p = .001$ and $p = .015$, respectively). By July that year, the difference

in cover between the disturbed and mown treatments had disappeared (arcsine-transformed data, $p > .05$). However, the average of the mown and disturbed treatments had lower cover than 'no treatment' plots ($p = .007$). This pattern persisted into 1989, so that in June 1989, arcsine-transformed percent cover data again showed no difference between mown and disturbed treatments. A significant difference was present in average cover in these treatments compared to 'no treatment' ($p = .0005$). This difference was reflected in the relative percent light readings in July 1989, when 'no treatment' plots had lower light levels at 5 cm and 15 cm heights (arcsine-transformed, $p = .0001$).

Analysis of soil moisture readings indicated that 'heavy disturbance' and 'mown more than once' plots were wetter (about 3 to 5 centibars) than 'no treatment' plots, and 'heavy disturbance' plots were wetter than 'light disturbance' plots (about 4 centibars, $p = .02$) in June 1988, but in July 1988 no differences were detected (Dunnett's test, $p > .05$). No significant differences were found among treatments in soil chemistry or organic matter ($p > .05$).

G. crinita plots did not differ in the incidence of herbivory in October 1988 between treatments (arcsine-transformed, $p > .05$). However *D. carota* did show some differences. 'No treatment' plots had slightly greater herbivory than the average of other treatments ($p = .0490$) and significantly more herbivory than plots mown once a year (Dunnett's test, $p < .05$).

Experiment in the scrub

Seedling Emergence

In 1988, emergence of *G. crinita* was significantly higher in the disturbed plots ($p = .038$) than the undisturbed plots, but *D. carota* showed no difference ($p > .05$). Significantly more *G. crinita* seedlings emerged in the scrub compared to *D. carota* ($p = .0001$).

Very few seedlings emerged in 1989 (Table 3.3) and neither species showed a significantly different response to the two treatments ($p > .05$). More *D. carota* seedlings emerged than *G. crinita* seedlings ($p = .02$) but the actual numbers were all low (maximum of 8 per plot). No seedlings emerged in the unseeded plots.

Establishment and size in 1988

Neither species differed between treatments or when establishment of the two species during 1988 was compared. Within each species, there were no significant differences in rosette diameter in the two treatments at the end of 1988 ($p > .05$).

Survival over winter and in 1989

The most striking result of the experiment was the very high mortality of both species over the winter. For *G. crinita* only 6 out of 171 plants alive in October were present in May, and only 5 out of 56 for *D. carota*. All had died by September 1989.

Table 3.3. Experiment in the scrub at the Natural Area: mean responses of *Gentianopsis crinita* and *Daucus carota* to the treatments. Means are back-transformed from data transformed by arcsine square roots (*), or natural logarithms (†). Because transformations may result in asymmetric back-transformed standard errors, the back-transformed range of ± 1 standard error around the mean is given (i.e. the difference between mean + 1 s.e. and mean – 1 s.e.).

	<u>Disturbed</u>		<u>No treatment</u>	
	Mean	Range ± 1 s.e.	Mean	Range ± 1 s.e.
% Emergence 1988 *				
<i>G. crinita</i>	32.8	13.1	18.9	6.3
<i>D. carota</i>	6.1	6.7	4.8	3.4
% Emergence 1989 *				
<i>G. crinita</i>	0.2	0.3	0.04	0.2
<i>D. carota</i>	0.8	1.4	1.2	0.9
% Establishment *				
<i>G. crinita</i>	30.0	14.6	33.8	10.8
<i>D. carota</i>	42.5	30.7	36.6	16.1
Size October 1988 † (rosette diameter in mm)				
<i>G. crinita</i>	10.7	1.7	8.8	1.6
<i>D. carota</i>	33.5	14.8	50.4	25.5

Environmental measures and herbivory in the scrub

There were no differences between the treatments in terms of percent cover of understory plants, relative light intensity, soil chemistry, and organic matter. No differences were found in the incidence of herbivory between or within the two species' comparisons. The soil in the disturbed plots was drier in July 1988 than the undisturbed plots (4 centibars difference between means, $p = .02$), although there had been no difference in June 1988 ($p > .05$).

Comparison of species performance, environment and herbivory between the clearings and tall scrub

Emergence, size and survival

Although sample sizes were somewhat disparate in the two experiments, the results of comparisons of these life history characteristics in the clearings and scrub were consistent with the trends apparent in the analyses of the individual experiments, even though a conservative non-parametric test was

used (Mann-Whitney). Treatments within an experiment were only combined when they had not been found to differ.

The pattern of emergence and establishment across all seven treatments for each species is shown in Fig. 3.5 and Fig. 3.6. The results in Table 3.4 indicate that *G. crinita* showed no significant difference in emergence response between clearings and scrub, whereas *D. carota* emerged in higher numbers in the treatments in the clearings. *D. carota* established much better in these plots, even where the ground was undisturbed and the vegetation unmown (Table 3.4). Greater establishment of *G. crinita* occurred in the 'mown more than once' treatment than in the scrub, but there was no difference between the tall scrub and 'no treatment' plots in the clearings (Table 3.4).

Both species grew larger in most or all treatments in the clearings (Table 3.4). As an illustration, the difference in size distribution of *G. crinita* rosettes in the clearings and the scrub is shown in Fig. 3.7. Of course the most striking difference between the two areas in the life history characteristics of the two species was the death of all the plants of both species in the tall scrub before they could reproduce.

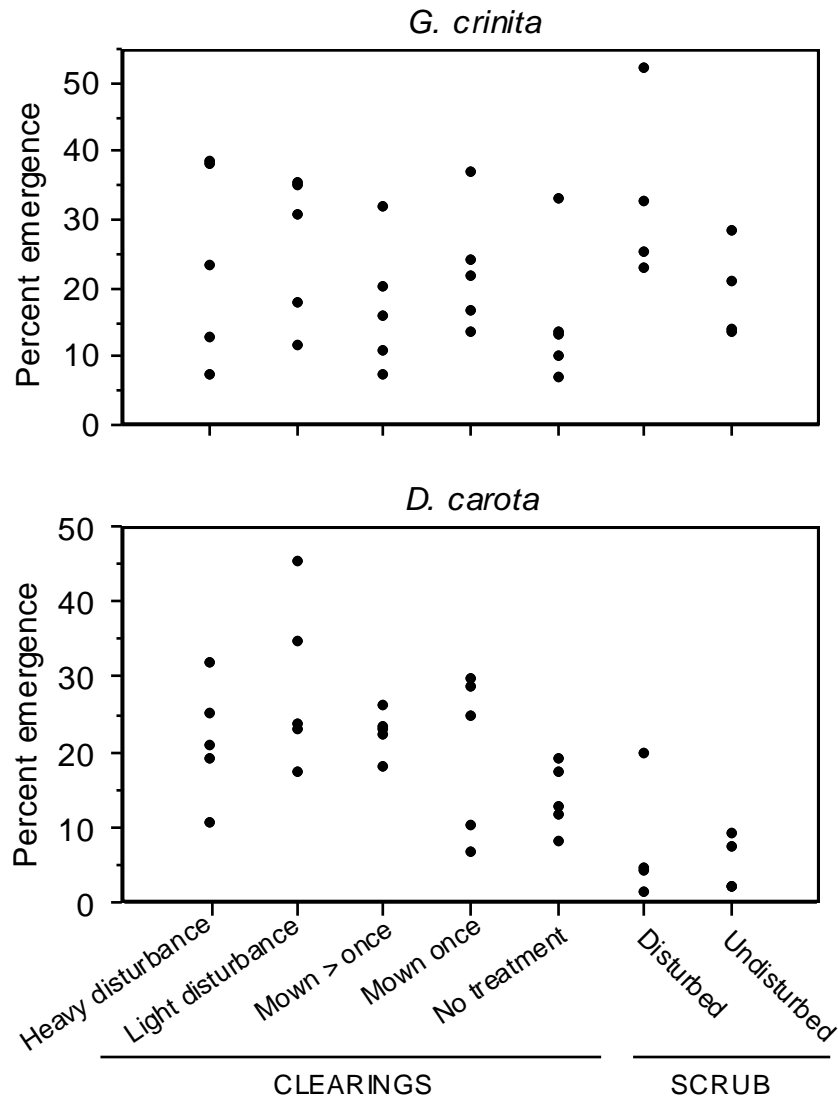


Fig. 3.5. Pattern of emergence of *G. crinita* and *D. carota* across all treatments in the Natural Area. The graphs show the percent emergence in 1988 (out of 300 seeds sown in November 1987) in each plot in each treatment.

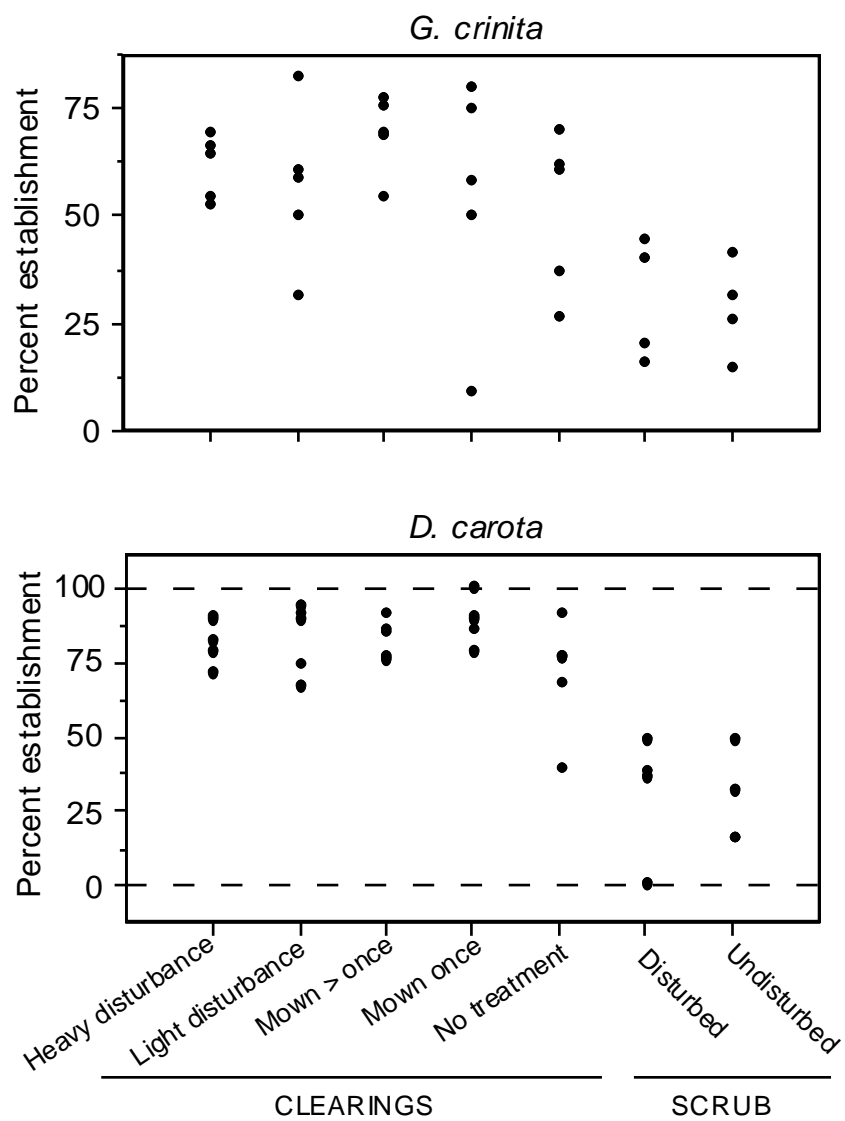


Fig. 3.6. Pattern of establishment of *G. crinita* and *D. carota* across all treatments in the Natural Area. The graph shows the percent establishment of seedlings that emerged, i.e. survival of seedlings to October 1988, in each plot in each treatment.

Table 3.4. Performance of *Gentianopsis crinita* and *Daucus carota* in the tall scrub compared to performance in the existing clearings at the Natural Area (Mann-Whitney tests). Sample sizes are shown in parentheses.

	Tall Scrub	vs.	Clearings	p value
<u>% Emergence in 1988</u>				
<i>G. crinita</i>	Disturbed plots (4)		Disturbed + Mown (20)	ns
	Disturbed plots (4)		No treatment (5)	ns
	Undisturbed plots (4)		Disturbed + Mown (20)	ns
	Undisturbed plots (4)		No treatment (5)	ns
<i>D. carota</i>	All plots (8)	<	Disturbed + Mown (20)	.0002
	All plots (8)	<	No treatment (5)	.040
<u>% Establishment in 1988</u>				
<i>G. crinita</i>	All plots (8)	<	Mown > once (5)	.003
	All plots (8)		No treatment (5)	ns
<i>D. carota</i>	All plots (8)	<	Disturbed + Mown (20)	<.0001
	All plots (8)		No treatment (5)	.008
<u>Average size</u>				
<i>G. crinita</i>	All plots (8)	<	All plots (25)	<.0001
<i>D. carota</i>	All plots (7)	<	Disturbed + Mown (20)	.0006
	All plots (7)		No treatment (5)	ns

ns = not significant at p = .05.

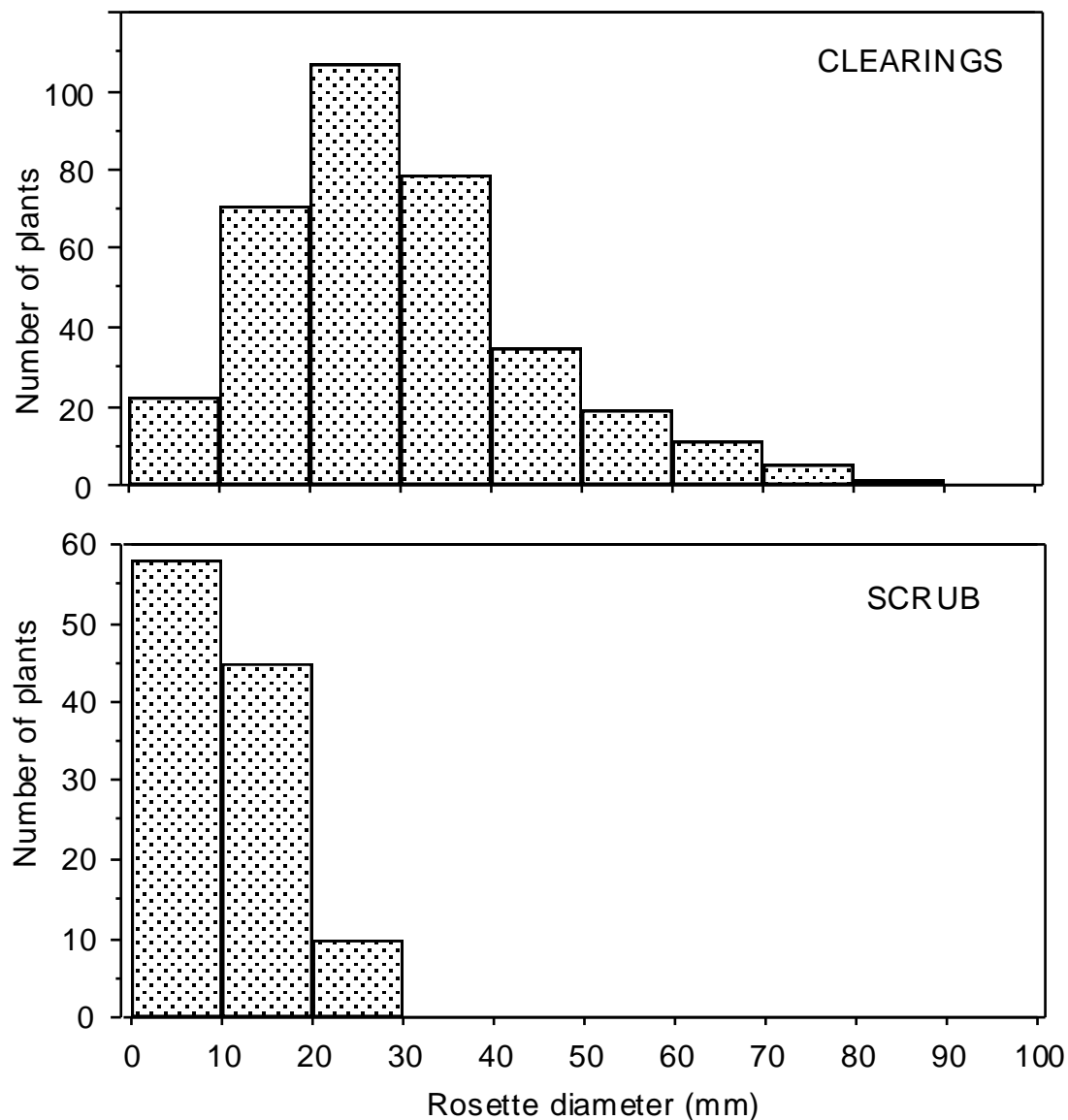


Fig. 3.7. Frequency distribution of rosette diameters of *G. crinita* in October 1988, in the existing clearings and scrub at the Natural Area.

Environmental measures and herbivory

Relative light intensity did not differ in July 1989 at 5 cm height between the tall scrub and 'no treatment' plots in the clearings ($n = 24$, $n = 15$, respectively, $p > .05$) but was lower in the scrub compared to the other treatments ($p < .0001$, $n = 24$, $n = 60$, respectively). At 15 cm height light levels in all plots in the clearings were higher than under the scrub, though the difference was only weakly significant in the case of the 'no treatment' plots (scrub vs. no treatment, $p = .046$; scrub vs. disturbed and mown plots, $p < .0001$).

The soil in the clearings was drier in June 1988 than soil in the scrub (e.g. scrub vs. 'no treatment', $p = .003$; $n = 24$, $n = 15$) except for 'heavy disturbance' plots and 'mown more than once' plots, which were not different compared to the scrub ($p > .05$). No differences were apparent in July 1988 (e.g. undisturbed or disturbed scrub plots versus 'no treatment' plots in the clearings, $p > .05$). Soil

chemistry and organic matter were different in the scrub compared to the clearings (Table 3.5). Levels of phosphorus, magnesium, calcium, manganese and organic matter were higher in the clearings. The incidence of herbivory in the two areas showed no significant differences ($p > .05$).

Table 3.5. Comparison of soil chemistry and organic matter in the tall scrub and existing clearings at the Natural Area (Mann-Whitney tests). Sample sizes were 8 plots in tall scrub, 25 in clearings.

Soil factor	Medians		Mann-Whitney p value
	Tall scrub	Clearings	
	<u>ppm</u>	<u>ppm</u>	
Phosphorus	0.3	0.5	.0008
Potassium	67	67	ns
Magnesium	160	237	.0005
Calcium	1253	1787	.002
Iron	33	18	ns
Aluminum	74	44	.004
Manganese	12	21	<.0001
Zinc	0.71	0.74	ns
pH	5.5	5.9	ns
loss on ignition (organic matter)	7.6 %	8.6 %	.008

ns = not significant at $p = .05$

Discussion

The two experiments produced an extensive set of results to interpret. To assist this interpretation the results are summarized in Table 3.6, which describes the responses of the 2 species in terms of their life history characteristics, in relation to different levels of disturbance and competition in the clearings and scrub.

Table 3.6. Summary of the responses of *G. crinita* (Gc) and *D. carota* (Dc) to various levels of disturbance and competition in the existing clearings and scrub at the Natural Area. Treatments in the clearings were: heavily disturbed ground + low levels of competition (HD), lightly disturbed ground + low levels of competition (LD), low levels of competition (M2), moderate levels of competition (M1), and high levels of competition (NT). Treatments in the scrub, under very high levels of competition from large woody plants, were: disturbed, i.e. litter removed (D), and undisturbed (NT). (Abbreviations are as in Figs. 3.2 and 3.3, which show examples of the experimental layout).

Life history characteristics	<u>Differences among treatments</u>		Relative performance (Gc vs. Dc)
	<i>G. crinita</i>	<i>D. carota</i>	
a) Existing clearings			
Seedling emergence in first year	<i>ns</i>	Slightly greater where ground disturbed and competition reduced vs. where competition high	<i>ns</i>
Seedling emergence in second year	More where ground heavily disturbed + low competition	<i>ns</i>	Not assessed*
Timing of seedling emergence (1 trt. only)	-	-	Dc earlier
Establishment in 1988	Maybe greater where low rather than moderate competition	Greater where ground lightly disturbed + low competition. Greater in moderate vs. high competition	Dc greater
Size in October 1988	<i>ns</i>	Larger on average where ground disturbed and competition reduced vs. high competition. Larger in heavily disturbed vs. lightly disturbed plots.	-
Overwinter survival	Maybe greater on average where ground disturbed & competition reduced vs. high competition plots. Greater in low vs. moderate competition plots.	<i>ns</i>	Dc greater
Survival in 1989	Maybe greater where low vs. moderate or high competition	<i>ns</i>	<i>ns</i>
Survival over 2 years	Maybe greater where ground heavily disturbed + low competition, and where low competition (undisturbed) vs. high competition	Greater where ground lightly disturbed + low competition, and where moderate competition vs. high competition	Dc greater
Reproductive output	Greater where ground disturbed + low competition, and where low (undisturbed) vs. high competition	Greater especially where ground disturbed + low competition, and where low (undisturbed) vs. high competition	Gc greater
<i>ns</i> = no difference * Interaction in factorial analysis; main effect could not be assessed.			

Table 3.6. (continued)

Life history characteristics	<u>Differences among treatments</u>		Relative performance (Gc vs. Dc)
	<i>G. crinita</i>	<i>D. carota</i>	
b) Scrub			
Seedling emergence in first year	Greater where ground disturbed vs. undisturbed	<i>ns</i>	Gc greater
Seedling emergence in second year	<i>ns</i>	<i>ns</i>	Dc greater
Establishment in 1988	<i>ns</i>	<i>ns</i>	<i>ns</i>
Size in October 1988	<i>ns</i>	<i>ns</i>	-
Survival Oct. '88-Sept. '89	All died	All died	<i>ns</i>
Life history characteristics	<u>Differences between scrub and clearings</u>		
	<i>G. crinita</i>	<i>D. carota</i>	
c) Scrub vs. clearings			
Seedling emergence in first year	<i>ns</i>	Greater in clearings	
Establishment in 1988	Greater where ground disturbed and competition reduced in clearings vs. very high competition in scrub. No difference between high competition in clearings and very high competition in scrub.	Greater in clearings	
Size in October 1988	Larger in clearings	Larger where ground disturbed and competition reduced in clearings vs. very high competition in scrub. No difference between high competition in clearings and very high competition in scrub.	
Survival over 2 years	Survival in all treatments in clearings, vs. no survival in scrub	Survival in all treatments in clearings, vs. no survival in scrub	

Seedling emergence

Neither species appeared to require disturbance to stimulate seedling emergence. In other studies *D. carota* emerged in disturbed, bare ground and undisturbed old field vegetation, but usually in greater numbers in bare patches and in fields that were in earlier rather than later stages of succession (Holt 1972, Gross & Werner 1982, Gross 1984, Goldberg 1987). The lower emergence in the scrub, and in

the untreated plots in the clearings, compared to treatments in the clearings where competition was reduced, is consistent with this trend toward lower emergence during later successional stages.

G. crinita did not require disturbance to stimulate seedling emergence, although this was sometimes enhanced by disturbance. Seedling emergence was not inhibited in the tall scrub – indeed the highest proportion of emergence per plot was seen in a plot in the scrub, albeit one that had been disturbed. *G. crinita*'s behavior is in contrast to other small-seeded biennials such as *Oenothera biennis* and *Verbascum thapsus*. Most seedlings of these species emerge in open bare patches in fields in the early stages of succession (Gross 1980, 1984, Gross & Werner 1982). *G. crinita* also differed from the biennial *Gentianella amarella* which emerges only in the shortest turf in English chalk grasslands (Kelly 1989b).

Size, survival and flowering

D. carota displayed behavior consistent with that seen in other studies of the species. Its survival was not always higher where there was less competition. Grubb (1976) noted that *D. carota* can maintain itself in tall turf in chalk grassland in England. During et al. (1985) found that seedling mortality was not correlated with vegetation density in chalk grassland in The Netherlands. Goldberg (1987) could find no significant differences in survival in gaps compared to undisturbed old field vegetation. It is likely that *D. carota* can colonize mid-successional habitats and can persist for a relatively long time in habitats undergoing succession. Pickett (1982) recorded its continued presence after 20 years of old field succession in New Jersey. It was found in a 30 year old field in Michigan (Goldberg 1987) and in fields of 6 age classes extending from 1 year to 60 years old in New Jersey (Bard 1952).

Rosette diameter and flowering in *D. carota* were affected by the treatment, as both responded positively to reduced competition in the disturbance and mowing treatments. Using a different measure of size (root crown diameter) Gross (1981) found that rosettes grew larger in a one year old field compared to 5 or 15 year old fields and that they had a higher probability of flowering the following year. Holt's study (1972) showed that reproduction began in the first growing season in sparsely vegetated plots of a younger fallow field but was delayed until the second year in an older fallow. Holt also found that more plants flowered in clipped than unclipped plots in fields of both ages. Gross and Werner (1982) noted no difference in rosette size (root crown diameter) between open and vegetated patches of an old field in both one and 15 year old fields, but flowering behavior paralleled the behavior of *D. carota* in the experiment in the clearings at the Natural Area. Here more plants flowered where the ground had been disturbed and interspecific competition reduced. In Gross and Werner's study a larger proportion of rosettes in the more recently disturbed field flowered compared to the proportion flowering in the older fallow field.

G. crinita was able to survive and flower in all treatments in the clearings, but not in the scrub. This finding is in accord with most published information about habitats occupied by *G. crinita*, which referred to its association with open conditions (e.g. Graves et al. 1910, Dean 1940, Andreas & Cooperrider 1981). My results contrast with some of the literature sources, which list low-lying woods and thickets as habitats (Torrey 1843, Gleason 1952, Scoggan 1957). These authors did not specify whether *G. crinita* occurred under dense canopies of woody species, as opposed to close to edges of scrub or in relatively open woodland. The latter distribution would be consistent with the results described above in Section I, and the findings of a survey of sites in New York State, described in Chapter 5.

G. crinita's survival and reproduction in all treatments in the clearings at the Natural Area contrast with the behavior of *Oenothera biennis* and *Verbascum thapsus*. Both have flat rosette-type seedlings similar to *G. crinita* but it seems that neither can survive and reproduce except in bare open patches (Gross 1980, Gross & Werner 1982).

Other biennial members of the Gentianaceae are found in semi-open herbaceous swards rather than in open bare ground (data from Salisbury 1942, Clapham et al. 1987), or can occur in closed herbaceous swards (Karlson 1974, Spira & Pollack 1986). Karlson suggested that, in Europe, the association of mycorrhizal fungi with species in the Gentianaceae might be important in allowing these species to survive in closed herbaceous swards, which lack open bare ground, but gave no conclusive data. Although gentians can survive in these habitats, such conditions may not be the most favorable. The survival of *Gentianella amarella* was greater and flowering success was higher in shorter rather than taller turf in English chalk grassland (Kelly 1989b). Similarly, *G. crinita*'s overall survival and reproductive output were greater where levels of competition were reduced in the disturbance and mowing treatments. Like other biennials, including *D. carota* (Gross 1981, and my study), *G. crinita*'s survival over winter was size related. A proximal cause of the massive mortality in the scrub was probably the small size attained by rosettes before the winter of 1988-89 (Fig. 3.7).

Environmental and biotic factors

Although the environmental and biotic factors that might affect the relative performance of the species within treatments were not intensively studied, the results provide some clues that could be followed up in further experiments.

The consistently lower plant cover and higher light in mown and disturbed plots in the clearings may have strongly influenced *D. carota*'s response. In the heavily disturbed plots in particular, the species may have been able to exploit the conditions of lower aboveground competition and perhaps also low belowground competition that existed for a short period in the spring of 1988. As the 1988-89 study of the timing of emergence demonstrated, *D. carota* does begin to emerge earlier than *G. crinita*, i.e. in late April or early May. Thus *D. carota* might be able to take better advantage of the window of opportunity provided by the disturbance treatments. *G. crinita* may not have been able to take such marked advantage of a relatively short-lived disturbance, although the results suggest that it may not need to, as it is able to reproduce successfully without such disturbance. However, the largest number of seedlings to emerge in the second year appeared in the heavy disturbance plots. This treatment may therefore have a more long-term effect on the population by enhancing emergence in the second year after seeds are dispersed, and thus increasing population size and potential reproductive output in later years. This finding is discussed further in Section III of this chapter.

Herbivory did not appear to have markedly different effects in different treatments, with the exception of *D. carota*'s 'mown once' plots versus 'no treatment' plots. Perhaps the greater establishment in these mown plots was influenced by the lower incidence of herbivory.

Higher levels of soil moisture in the 'heavy disturbance' and 'mown more than once' plots in June 1988 do fit the pattern of *G. crinita*'s greater survival and ultimately greater reproduction in these plots. Seedlings are likely to be particularly vulnerable to drought at that early stage and results from the Radio Lab site (to be discussed in Chapter 5) suggest soil moisture is a key factor affecting *G. crinita*'s performance.

Availability of soil nutrients seemed to be little affected by treatments in the long term, i.e. after two years, either within the clearings or the scrub. There may have been transient differences between the treatments that could have influenced the two species, but these differences were not picked up by the soil analyses which were done on samples collected at the end of the experiment. However the soil analyses did show generally lower nutrient levels in the scrub compared to the clearings. The interaction of lower levels of light, because of shading by tall woody plants, and lower levels of soil nutrients in the scrub could have reduced growth of both species to such an extent that survival to completion of the life cycle was not possible. Grubb (1989) emphasized the importance of this kind of interaction and gave an example from Ellenberg's work in 1939 which showed greater toleration of deep shade by woodland herbs when nutrient status was higher.

To summarize, *D. carota* was able to exploit an increase in resources made available through disturbance but could also survive in dense vegetation. *G. crinita*'s performance was better in undisturbed, dense herbaceous vegetation compared to some other common biennials, and *G. crinita*'s response was similar to that of other members of the Gentianaceae. In comparison with *D. carota* it appeared to be more susceptible to competition in its vegetative stage, as survival was lower than that of *D. carota* across all treatments in the clearings. However, *G. crinita* was able to reproduce within two years in all these treatments and produced many more flowers than the number of umbels produced by *D. carota*. Relative reproductive output is examined in detail in Chapter 4, but results indicate that *G. crinita* can produce at least twice the seed numbers per flower head compared to seeds per umbel of *D. carota*. *G. crinita*'s greater frequency of flowering, more flower heads, and seeds per reproductive head would therefore seem to give the species a much greater potential for population increase compared to *D. carota*, even where levels of interspecific competition are high.

Delayed flowering is often seen in common biennial species (Holt 1972, Werner 1975b, van der Meijden & van der Waals-Kooi 1979, Gross 1981). Klinkhamer and de Jong (1983) propose that this paradox, of species that are abundant yet have infrequent reproductive events, might be resolved if variability over time in the number of offspring is taken into account. Such variability could be caused by environmental fluctuations. Their model suggests that delay in flowering might become advantageous, for instance if seedlings are more vulnerable to fluctuations in moisture supply than are older plants. Thus if a drought had occurred in the Natural Area in 1990, it might have caused high mortality among *G. crinita* seedlings that originated from seed shed in 1989, while older *D. carota* rosettes of the 1987 cohort might have been able to survive reasonably well. Results given in Section II of Chapter 5 indicate that *D. carota* rosettes more than 1 year old do survive drought conditions better than seedlings of *D. carota* or *G. crinita*.

However, under the experimental conditions in 1987-89, *G. crinita* demonstrated its ability to cope with a wide range of intensities of disturbance and competition. These results suggest that the failure of previous conservation attempts in the clearings was not directly due to lack of disturbance or because the successional habitats created by scrub clearance were unsuitable. Extension of the conclusions about the experiments to natural successional situations implies that *G. crinita* can survive through a similar range of stages as a common biennial and can reproduce even in mid-successional stages dominated by tall herbs and low shrubs. However neither the scarce, nor the common, biennial can survive later stages of succession when taller woody species predominate.

SECTION II. REGENERATION IN SITES WITH EXISTING POPULATIONS OF *G. crinita*

Introduction

Biennials have to rely on seeds and seedlings for regeneration within an existing population as they have no means of vegetative reproduction. The critical importance of the regeneration phase of the life cycle in allowing plant species to co-exist has been emphasized by Grubb (1977). There have been several comparative studies of the differences in conditions under which regeneration by seed occurs among groups of species that occupy the same habitat (e.g. Miles 1974, Fenner 1978, Silvertown 1981, Gross & Werner 1982, Verkaar & Schenkeveld 1984a). Grubb et al. (1982) suggested that one of the explanations for differences in relative abundance of short-lived species might be that the microsites suitable for the establishment of rare plants are less extensive than those suitable for abundant species. Gross and Werner (1982) found that the relative abundance of four common biennials that colonized old fields was controlled by the relative abundance of particular microhabitats.

D. carota may be more abundant than *G. crinita*, in habitats where established populations of both species occur, because it can successfully regenerate in a range of widely available microhabitats. In

contrast *G. crinita* might require a scarce microhabitat. This section of the chapter examines the hypothesis that *G. crinita* is restricted in abundance, within those successional habitats where it can survive, by a scarcity of suitable microhabitats for colonization and regeneration.

Materials and Methods

Recording of regeneration of *G. crinita* and *D. carota* in different microhabitats was undertaken at the Radio Lab field and at Letchworth State Park.

Experimental layout

The Radio Lab site was a more or less level old field, dominated by herbaceous species that were generally less than 25 cm in height. The landslip at Letchworth was a series of sloping banks dissected by small gullies and had a mosaic of bare ground, herbaceous vegetation, and scrub. It may have been an example of one of the natural habitats occupied by *G. crinita*, as opposed to the old field site which most likely was once forest before clearance for agriculture. Both sites had populations of *G. crinita* and *D. carota*. The sites are described more fully in Chapter 2.

The experiments and observations were designed to be comparable to Gross and Werner's (1982) study of the colonizing ability of four common biennials, including *D. carota*, in different microhabitats in old fields in Michigan. At the Radio Lab field, a 50 by 30 m area within the *G. crinita* population was defined and 60 randomly located plots laid out in the fall of 1986. Each plot measured 20 by 20 cm. Twenty plots were seeded with 1000 seeds each of *G. crinita*, twenty plots with 1000 *D. carota* seeds each, and twenty were left unseeded. The seed was scattered within each plot as evenly as possible. The seed was collected in the fall from the surrounding area and sown almost immediately. The decision about seed number per plot was made in the absence of data on possible germination rates of *G. crinita* and potential losses over the winter. The number chosen was based on the rather low emergence of *D. carota* (2-13%) in Gross and Werner's experiment.

Between 8-17th June 1987, the emergence of seedlings was recorded in three categories of microhabitat: bare ground, moss, and vegetation plus litter. At the same time the percent cover of these three microhabitats in each plot was estimated by eye using a grid divided into 25 4 by 4 cm squares. A fourth category, bare rock, was also recorded. In July (19-20th) a sample of 50 randomly selected plants in each microhabitat for each species was marked by placing color-coded plastic covered wire near the seedling. The survival of these plants was recorded in mid to late October (18-23rd). Survival was followed into 1988 but almost all plants died in the drought that year so no data analysis was possible.

In the fall of 1987, the experiment was repeated, this time using 30 additional plots divided into two sets of 15. One set was sown with 150 *G. crinita* seeds and one set with 150 *D. carota* seeds. The number of seeds sown per plot was much lower than in 1986 because seedling emergence from the 1986 sowing had been unexpectedly high, resulting in seedling densities per plot that were not usually seen under natural conditions (*pers. obs.*). Emergence in the three microhabitats was recorded between 26th-31st May 1988 and the percent cover of the three microhabitats and rock was estimated. At the same time, the seedlings in the central 5 squares of the grid were marked and mapped (an area of 80 cm² per plot). The survival of these seedlings was recorded in early November 1988 (6-8th). Between 29th July and 1st August 1988 all other seedlings remaining in the plots were marked, to increase the sample size after it had been reduced by the drought. The survival of these seedlings and those marked in May was followed through to the end of August 1989 (31st August - 2nd September).

At Letchworth, four 10 m by 40 cm transects were laid out 1 m apart on the landslip, parallel to the slope, which had about a 25° angle (measured by a clinometer). Percent cover of microhabitats and

rock was recorded in 40 by 40 cm sections, i.e. a total of 100 quadrats, and the presence of every *G. crinita* seedling marked and mapped in late July 1987 (21st - 22nd). A subsample of 76 *G. crinita* seedlings in 2 transects had previously been marked at the end of June 1987 (29th - 30th). The population of *D. carota* seedlings was estimated on 21st and 22nd July by counts in 25 randomly selected quadrats and was found to be ten times the number of *G. crinita* seedlings (163) present in July. To achieve a sample of similar size, 163 *D. carota* plants were randomly selected and marked in the transects. Survival was followed through 1987, 1988, and until 1st October 1989. Both species were marked a fairly long time after emergence in some cases, but seedlings can be distinguished from older plants for most, if not all, of the first year. *G. crinita* is always a rosette in the first year but bolts in April or May the second year. *D. carota* has cotyledons for several weeks and later usually shows no sign of thickening of the root crown, at least until the end of the first growing season, in contrast to the thickened root crowns of plants more than one year old.

Data analysis

Data were analyzed using χ^2 tests to compare actual numbers of seedlings in each microhabitat with the numbers that would be expected if emergence was random and therefore in proportion to the percent cover of each microhabitat. It was assumed that no seedlings could emerge from the bare rock, so percent cover of the other three categories was adjusted to total 100%, i.e. equivalent to the total available microhabitat area. In addition to comparison between all three microhabitats, emergence in moss and bare ground was compared in 1987 and 1988. In common with Gross and Werner's (1982) study, the emergence of each seedling was assumed to be independent and the counts from all plots or transects within each experiment were combined for analysis of that experiment. Relative survival in different microhabitats was analyzed using χ^2 tests. Where expected values were too small to permit a legitimate χ^2 test to be made, binomial confidence intervals of the proportion surviving were calculated according to the method described in Blyth and Still (1983).

Results

Area of microhabitats

In the Radio Lab field, vegetation and litter was the most abundant microhabitat. On average this type covered around 65-75% of each plot, while bare ground was relatively limited, particularly in 1987, when on average less than 10% of each plot had bare ground (Fig. 3.8). In contrast, the Letchworth transects had much larger areas of bare ground (average 40%), which equalled the cover of vegetation and litter (39%, Fig. 3.8).

Seedling emergence

Unexpectedly high numbers of seedlings emerged in the Radio Lab field in 1987 from the 1000 seeds per plot sown in 1986. Over 4000 *D. carota* and nearly 3000 *G. crinita* seedlings were counted in the plots, and most plots had over 100 seedlings (Table 3.7). Although very dense patches of seedlings can occur naturally (pers. obs.), it is not usual to have on the order of 100 seedlings in an area of 400 cm². The repeat experiment in 1988, when 150 seeds were sown per plot in 1987, gave considerably lower seedling densities per plot (Table 3.7). As explained in the methods (above), the 1986 sowing rate was based on the rather low emergence of *D. carota* in Gross and Werner's experiment. They collected their seeds of *D. carota* in the fall and sowed them in the following spring, when emergence was recorded (Gross & Werner 1982), and apparently stored the seeds inside over winter. It may be that germination of *D. carota* was enhanced in my study by sowing seeds in the fall and overwintering them in the soil rather than by storing them in the laboratory.

Only 13 *G. crinita* seedlings emerged in the unseeded plots at the Radio Lab in 1987, but over 400 *D. carota* seedlings appeared. A χ^2 analysis of *G. crinita* in unseeded plots was thus not possible, but was for *D. carota*.

Emergence of *G. crinita* was strongly influenced by microhabitat type in both sites and years (Fig. 3.8). Fewer seedlings emerged in the vegetation and litter than expected and more in the moss and bare ground types. *D. carota* showed a rather less marked pattern of emergence in 1987. The unseeded plots showed no difference, while the large sample in the seeded plots in 1987 at the Radio Lab may have enabled a very slight difference to be detected in behavior of *D. carota* in different microhabitats (Fig. 3.8b). At Letchworth in 1987 and at the Radio Lab in 1988, *D. carota* showed a similar pattern to *G. crinita*.

When moss and bare ground habitats were compared *G. crinita* only showed a difference at Letchworth where emergence occurred preferentially in the moss habitat. For *D. carota*, the unseeded plots or transects showed no differences. However, at the Radio Lab in 1987 and 1988, the seeded plots had more emergence in bare ground than moss (Table 3.8).

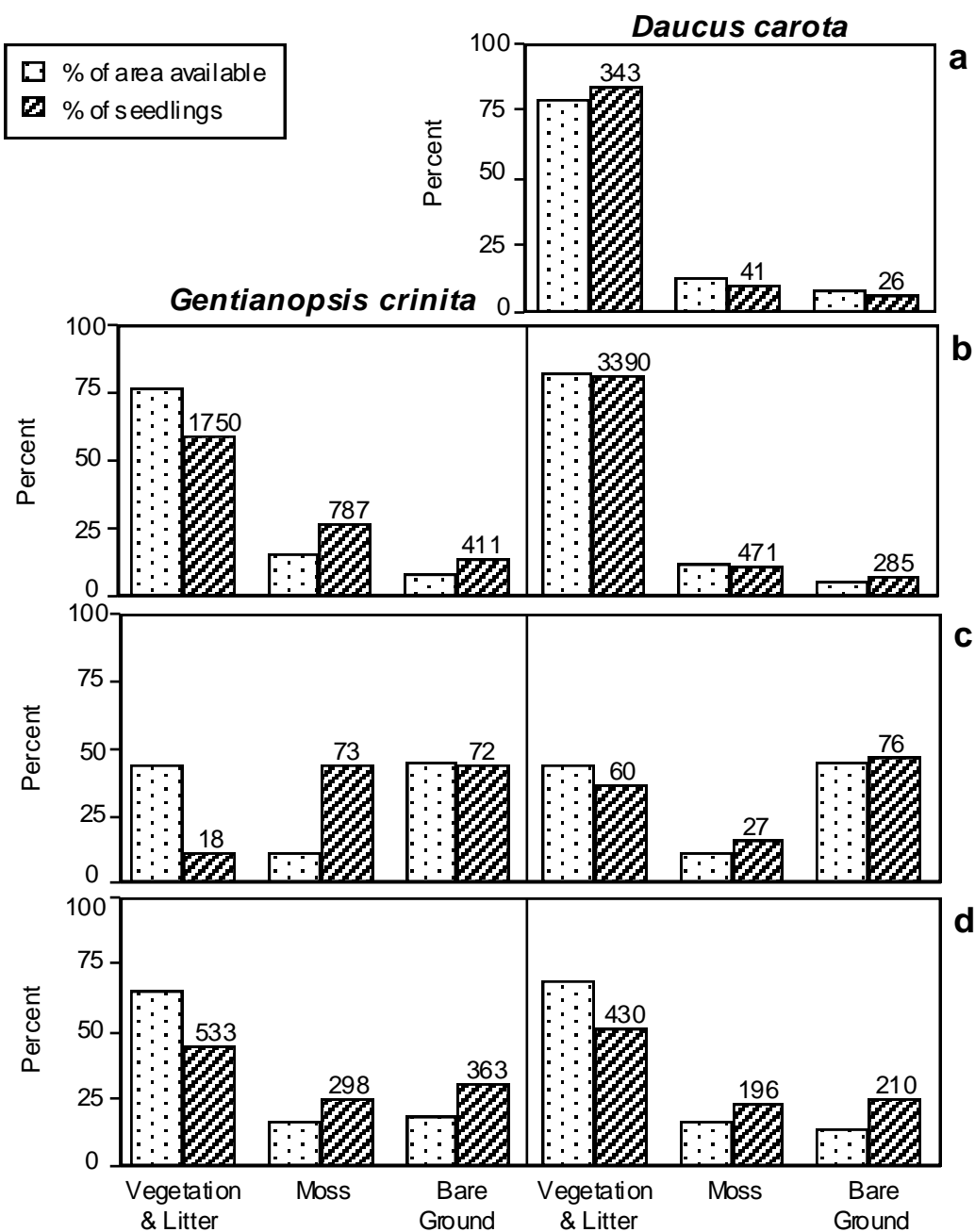


Fig. 3.8. Number of seedlings of *G. crinita* and *D. carota* (percent of total; actual numbers shown above each bar) compared to the proportion of the ground in each microhabitat (excluding 2 to 11% area in rock), in the:

- a) Radio Lab unseeded plots in 1987 (chi-squared $p = .054$, for *D. carota*, observed seedling number vs. expected based on available area), *G. crinita* is not shown, as only 13 seedlings were present,
- b) Radio Lab seeded plots in 1987 ($p = .0001$ for each species),
- c) Letchworth unseeded transects in 1987 ($p = .0001$ for *G. crinita*, .03 for *D. carota*), and
- d) Radio Lab seeded plots in 1988 ($p = .0001$ for each species).

Table 3.7. Mean numbers (± 1 s.e.) of seedlings emerging per 20 x 20 cm plot in the Radio Lab experiments, which were set up to study regeneration of *G. crinita* and *D. carota* in different microhabitats (n = 20 plots in 1987, n = 15 in 1988). The 1987 seedling emergence was from 1000 sown seeds per plot plus any native seeds. The 1988 emergence was from 150 sown seeds per plot plus any native seeds.

	<i>Gentianopsis crinita</i>	<i>Daucus carota</i>
1987 (seeded plots)	147 \pm 17	207 \pm 19
1987 (unseeded plots)	0.7 \pm 0.4	21 \pm 5
1988 (seeded plots)	77 \pm 13	56 \pm 8

Table 3.8. Comparison of seedling emergence of *G. crinita* and *D. carota* in moss vs. bare ground microhabitats, relative to expected emergence based on the proportion of area of moss or bare ground.

	<u>Observed numbers vs. expected</u>			
	Moss	Bare ground	χ^2	p value
<i>Gentianopsis crinita</i>				
Radio Lab 1987 (seeded)	-	-	0.14	.71
Letchworth 1987 (unseeded)	More	Less	90.50	.0001
Radio Lab 1988 (seeded)	-	-	0.33	.57
<i>Daucus carota</i>				
Radio Lab 1987 (seeded)	Less	More	21.70	.0001
Radio Lab 1987 (unseeded)	-	-	0.02	.89
Letchworth 1987 (unseeded)	-	-	3.25	.07
Radio Lab 1988 (seeded)	Less	More	9.24	.002

Seedling survival

Very few *G. crinita* plants died during the 1987 season at the Radio Lab, and no difference was seen between percent survival of first-year plants in the three microhabitats (Table 3.9). Although mortality at Letchworth in 1987 was greater, there was again no difference between microhabitats. The survival of the June subsample showed a similar pattern. Survival was 43% in vegetation and litter, 47% in moss and 41% in bare ground. As might be expected, given the longer recording period, the survival percentages were slightly lower overall than the July to November figures. At the Radio Lab

field in the drought year of 1988, more seedlings of the 1988 cohort survived in bare ground than in the other microhabitats at the Radio Lab (bare ground vs. moss and vegetation + litter, $\chi^2 = 7.08$, $.005 < p < .01$; see Table 3.9 for overall χ^2). *D. carota* showed no differences in percent survival of first-year plants between microhabitats at the Radio Lab in 1987 and 1988 or at Letchworth in 1987 (Table 3.9).

It was not possible to assess relative survival over 2 years in different microhabitats for *G. crinita* and *D. carota* plants marked in 1987 at the Radio Lab field, because too few survived the 1988 drought. Few of the *G. crinita* seedlings marked in May 1988 survived until the flowering season in 1989. However, among the extra seedlings marked at the end of July 1988, no significant difference in survival in different microhabitats was seen by the end of August 1989 ($\chi^2 = 3.09$, $p > .05$). Plants in all categories produced flowers, and no plants remained as rosettes in the second year.

At Letchworth there was a trend toward higher survival of the 1987 cohort in vegetation and litter by the end of September (29th) 1988, but the difference was not significant (33% survival in vegetation and litter, 19.2% in moss, 18.1% in bare ground; confidence intervals overlapped). Flowers were present on plants in all categories and all plants produced elongated flowering stems in 1988. All plants died after flowering.

At the Radio Lab there was no difference in survival of *D. carota* rosettes (marked as seedlings in July 1988) by the end of August 1989, i.e. towards the end of their second season ($\chi^2 = 0.71$, $p > .05$). No plants marked in 1988 flowered in 1989. At Letchworth there was no difference in survival of the 1987 cohort between microhabitats by 1st October 1989 (confidence intervals overlapped). By this date 7 *D. carota* plants had flowered (3 in vegetation plus litter, 4 in bare ground).

Table 3.9. Percent survival of seedlings of *Gentianopsis crinita* and *Daucus carota* in vegetation and litter, moss, and bare ground microhabitats.

	Percent survival			χ^2	p value
	Vegetation & litter	Moss	Bare ground		
Radio Lab, July to November 1987					
<i>G. crinita</i>	84	88	92	1.51	.47
<i>D. carota</i>	62	54	72	3.49	.17
Letchworth, July to November 1987					
<i>G. crinita</i>	50	55	51	0.23	.89
<i>D. carota</i>	93	93	80	*	
Radio Lab, May to November 1988					
<i>G. crinita</i>	7	9	16	7.30	.03
<i>D. carota</i>	12	15	13	0.39	.82
Sample sizes:					
	Initial number of seedlings				
	Vegetation & litter	Moss	Bare ground		
Radio Lab, July 1987					
<i>G. crinita</i>	50	50	50		
<i>D. carota</i>	50	50	50		
Letchworth, July 1987					
<i>G. crinita</i>	18	73	72		
<i>D. carota</i>	60	27	76		
Radio Lab, May 1988					
<i>G. crinita</i>	148	105	143		
<i>D. carota</i>	137	92	115		

* Expected values for mortality too small for chi-squared test.

95% binomial confidence intervals are:

83 - 98 % survival in vegetation and litter,

77 - 99% survival in moss, and

69 - 88% survival in bare ground.

Discussion

Both species showed preferential emergence in moss and bare ground microhabitats compared to vegetation and litter. If the first two types are treated as "gaps," in the sense of ground not occupied by vascular plants and their litter, then *G. crinita* may show a stronger positive response to gaps than *D. carota* but only in some years. For example, in seeded plots in the Radio Lab in 1987, 41% of *G. crinita* plants and 18% of *D. carota* plants emerged in gaps, which occupied less than 20% of the available area in both cases. However, in 1988 55% of seedlings of *G. crinita* and 49% of *D. carota* emerged in gaps which covered some 35% of the available area.

Although increased regeneration of both species is associated with gaps, they can also regenerate successfully in closed, herbaceous vegetation. This finding parallels the results in Section I of this chapter. Those results showed that, at a larger scale of investigation, both species could survive in a range of early to mid-successional habitats. Other studies of *D. carota* also found that it could regenerate in closed vegetation (Holt 1972, Gross & Werner 1982). Gaps in old fields may be rare and short-lived (Goldberg & Gross 1988), so the ability of both species to regenerate in closed vegetation is an advantage compared to the inability of some species such as *Oenothera biennis* and *Verbascum thapsus* to tolerate dense vegetation (Gross 1980, Gross & Werner 1982).

Emergence of *G. crinita* seedlings was not consistently higher in moss compared to bare ground, and survival in moss was not greater. Keizer et al. (1985) could find no correlation between seedling emergence and survival with bryophyte cover for *Gentianella germanica* in chalk grassland. Removal of bryophyte cover the previous autumn also had no effect. However Giersbach (1937) found that in a greenhouse, *G. crinita* grew better in pots covered in moss, compared to growth in pots with bare substrate. The very strong positive association of seedling emergence of *G. crinita* with moss cover at Letchworth may be due to the physical action of the moss which might trap seeds washed down the slope. This point is examined further in Section III of this chapter.

D. carota tends to emerge in greater numbers in bare ground than in moss. When I analyzed data reported by Gross and Werner (1982) for *D. carota* in a 15 year old field, there was significantly greater emergence in bare ground than in moss and lichen cover ($\chi^2 = 155.92$, $p < .0005$).

Johnson and Thomas (1978) found that soil beneath moss patches was wetter than beneath bare areas in an abandoned pasture in Ontario, Canada. However their work suggests that the size and shape of the seeds may affect the response of a species in different microhabitats. These authors thought that the germination of their study species, *Hieraceum piloselloides*, might be inhibited in moss patches if the achene was suspended above the soil by the moss tufts. However if the seed was able to germinate and the roots reached the soil, then subsequent survival in dry periods should be enhanced by the damper moss-covered soil. It is possible that the small seeds of *G. crinita* could slip deep into well developed moss tussocks while the larger, spiny *D. carota* seeds would be caught above the soil surface, with the result that germination would be inhibited. Alternatively, emergence of *D. carota* seedlings may be more inhibited by higher moisture levels associated with moss-covered soil. Relative amounts of seedling emergence in moist and waterlogged substrates were studied in an experiment described in Section III of Chapter 5. The results suggest that emergence of *D. carota* is less in waterlogged conditions.

Gap size and location may also be important factors in successful regeneration. Neither my study nor Gross and Werner's (1982) research looked at individual gap sizes. Miles (1974) showed that gap size could affect seedling emergence and survival. He found that germination of heath plants was better in small gaps but later survival was lower than in large gaps. He suggested that smaller gaps may have a more equable microclimate, which would enhance germination. However, plants in small gaps would suffer increasing competition from vegetatively regenerating species, compared to plants in large gaps, so their later survival would be lower than that of plants in large gaps. The effect of

microtopography was not examined in Gross and Werner's experiment (1982) or in my study, although my casual observations suggested that there was no clear relationship between the distribution of *G. crinita* or *D. carota* seedlings and microtopography.

G. crinita appeared to be sparse in large bare areas (over several square meters) at the Radio Lab site and at Letchworth. The relationship between abundance of a species and the extent of the favored microhabitats is unlikely to be a simple one. The presence of more bare ground at Letchworth will not necessarily result in larger populations than at the Radio Lab site. In fact at Letchworth there were lower overall survival rates than at the Radio Lab field in 1987. Larger scale environmental patterns and other factors may override the effect of microhabitat. The greater survival of *G. crinita* in 1988 in the bare ground microhabitat at the Radio Lab field was likely to have resulted from the location of the plots with greater areas of bare ground in the wetter parts of the field. Again, in the drought of 1988 the potentially damper moss microhabitat was of no assistance to *G. crinita*.

To summarize, *G. crinita* does not require a specific, uncommon microhabitat, as defined by ground cover type, for successful regeneration. It can be favored by a greater abundance of particular microhabitats, i.e. bare ground and moss, though the presence of large expanses of bare ground does not necessarily mean that *G. crinita* will be abundant. It can survive well in a fine-grained mosaic of bare ground, moss, herbaceous vegetation and litter. It does not appear to be consistently more limited than *D. carota* in the range of microhabitats that it occupies. Indeed in some instances it appears to be less demanding, for instance as seen when seedling emergence in moss and bare ground at the Radio Lab field were compared.

Section III. Colonizing ability of *G. crinita* in relation to seed dispersal in time and space

Introduction

Gentianopsis crinita appears to be confined to unforested habitats, as are several common biennials, including *D. carota* (van der Meijden & van der Waals-Kooi 1979, Grubb 1976, Gross 1980, Grime et al. 1988). *G. crinita* was unable to survive in the later stages of succession from open ground to scrub in the Natural Area near Ithaca (Section I of this chapter). A survey of *G. crinita* localities in New York State (Section I of Chapter 5) and published information (e.g. Wiegand & Eames 1926, Andreas & Cooperrider 1981, Reed 1986, Mohlenbrock 1986) indicate that *G. crinita* is generally found in open habitats across its range. However, this range lies almost entirely within the forested eastern United States and Canada (Fig. 3.9). Thus the potential habitats available for colonization by *G. crinita* are patchy, as they are limited to land too dry or wet for trees, e.g. cliff tops and marshes, or to land cleared of trees by humans or by some natural disturbance such as a landslide. These open patches vary in their continuity. At one extreme some cliff top habitats might have persisted for several thousand years after the end of the last glaciation. At the other extreme, a forest clearing may only exist for a few years before vigorous regrowth and regeneration by woody species makes it unsuitable for herbaceous plants that require open conditions (Marks 1983).

Efficient seed dispersal in time and/or space allows a species to exploit patchy habitats. Hart (1977) suggested that biennials were particularly successful at colonizing intermittently available habitats. Biennials, such as *Verbascum thapsus*, can have persistent seed banks. Viable seeds of *V. thapsus* can persist for 50 to 100 years in the soil (Oosting & Humphreys 1940, Gross & Werner 1982). Other common biennials have efficient long-distance seed dispersal, e.g. *Senecio jacobea* and *Cirsium vulgare* (Grime et al. 1988). In contrast, Baskin and Baskin (1979) suggested that in Tennessee, the biennial species *Grindelia lanceolata* was restricted to a few localities by its lack of persistent seed bank and ineffective spatial dispersal of seeds. *G. crinita* may also be scarce because it has ineffective mechanisms for seed dispersal.

This section of the chapter examines the hypothesis that *G. crinita* is rare because it has limited colonizing abilities due to its poor seed dispersal capabilities. Experiments and observations were carried out to find out: 1) if *G. crinita* does have a persistent seed bank, which would therefore suggest that it has effective dispersal in time, and 2) whether it possesses characteristics that would imply efficient long-distance seed dispersal.

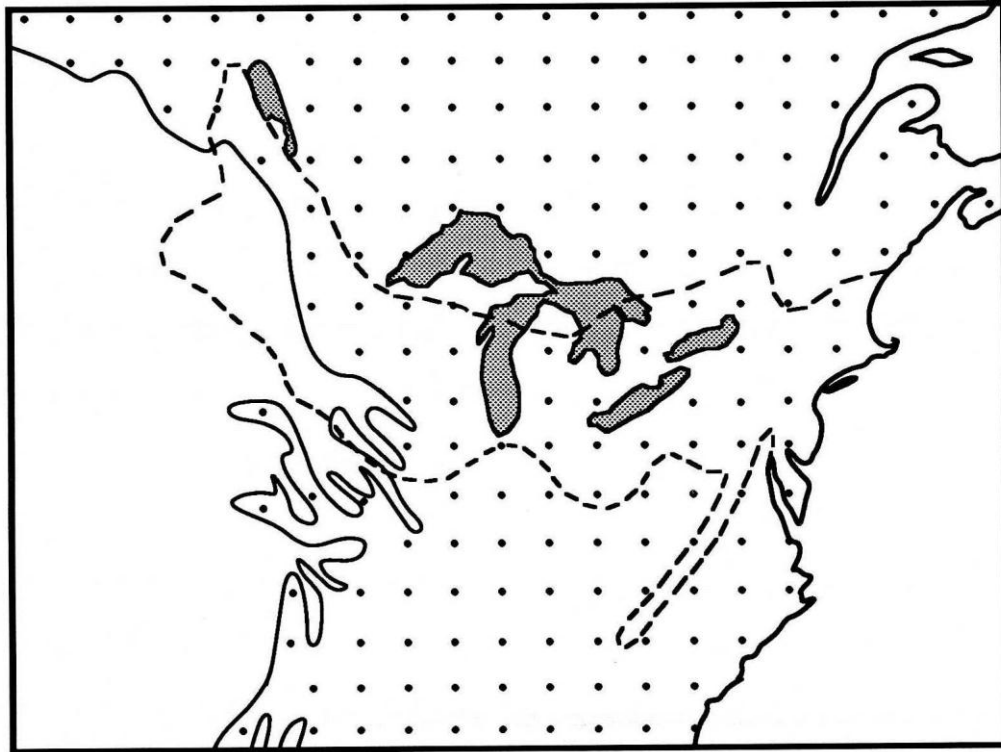


Fig. 3.9. Range of *Gentianopsis crinita* (- - - -) relative to the forest zone in eastern North America (••••), modified from Braun 1950, Iltis 1965, and Barbour & Billings 1988.

Dispersal in time: the seed bank of *G. crinita*

Introduction

The persistence of *G. crinita*'s seed bank was investigated in three ways. Existence of buried seed was assessed by clearing scrub at the Natural Area in a part of the preserve where there had been many gentians in the past and recording occurrence of *G. crinita*, and by recording seedling emergence from soil samples collected from this part of the preserve. Persistence of a seed bank was also studied by examining data on rates of decline in seedling emergence in successive years, derived from three field experiments, two in the Natural Area and one in the Radio Lab field. In addition, length of seed dormancy was investigated in the greenhouse by recording amounts of seedling emergence before and after stratification of seeds for various lengths of time. Comparisons with *D. carota* were made in most cases. When comparison with *D. carota* was omitted, relevant information was extracted from previous studies (Holt 1972, Dale 1974, Lacey 1978, 1982, Roberts 1986), and is described in the discussion that concludes this section of the chapter.

Buried seed bank: two experiments in the Natural Area

Methods

(1) To investigate whether *G. crinita* has a substantial buried seed bank that would respond to scrub clearance and soil disturbance, three 5 by 10 m plots in the northern part of the Area (plots A-C in Fig. 3.1) were cleared in November 1987 by clipping all woody stems at the base and then digging over the surface layer of soil with shovels. This part of the preserve had been described on a map made by Dorothy McIlroy in 1970 as having "many gentians" (Cornell Plantations information), so it seemed to be the location most likely to yield results if a long-term substantial seed bank did exist. A few plants were seen there in 1985 in very small openings. In 1987 none were found and the scrub appeared to be totally closed.

Regrowth of woody plants was cut back once in August 1988 and once in June 1989. In the fall of 1989 the plots were searched on three occasions for flowering *G. crinita* individuals. The plots were visited once more, in fall 1990.

(2) At the same time as the plots were cleared, in November 1987, 15 soil samples were taken along a transect to the south of plots A-C (Fig. 3.1). The samples were 2 m apart, beginning 5 m from the eastern edge of the scrub. Each sample consisted of the upper 5 cm of the soil in a block 10 cm by 10 cm. The samples were stored for 3 weeks in a refrigerator and then each was spread thinly over a 4 cm thick layer of Cornell mix in 25 by 50 cm trays so that any seeds would be close to the surface. Cornell mix is composed of 2 : 1 peatmoss : vermiculite, with 7.3 kg of fertilizer per cubic meter, in the ratio of 20 lime : 8 phosphate : 2 calcium nitrate : 2 potassium nitrate : 1 trace elements. Other experiments (described in Chapter 5) showed that *G. crinita* seed does remain on Cornell mix even when trays are overwintered outside. The 15 trays were placed on a flat roof at Cornell, watered as necessary to keep the soil moist. The trays were regularly inspected during the spring 1988 until the experiment was terminated at the end of June. A "control" was provided by *G. crinita* seeds sown on Cornell mix in trays and also kept on the roof over winter.

Results

(1) During the fall of 1989, a total of three flowering plants was seen in the three 5 x 10 m plots A-C. Of these three plants, one occurred in plot B and was uprooted, probably by a deer, before seed set. The other two plants were in plot C and both had four flowers each. All the flowers were nipped off one plant before seed set, again probably by deer, while the other lost two flowers. The impact of herbivory on flowering plants of *G. crinita* is explored further in Chapter 4. The remaining two flowers set seed, which was dispersing by mid-November. No flowering individuals were seen in 1990.

(2) No seedlings of *G. crinita* appeared in the trays overwintered outdoors, although other species emerged. It should be noted that seedlings did emerge in the "control" trays on the roof over this period (see Section III of Chapter 5).

Rate of decline in seedling emergence over time: field experiments

An indication of the "decay rate" of *D. carota* and *G. crinita* seeds in the uppermost layer of the soil was obtained from the seedling emergence percents in successive years, from seeds sown in 1987 in the Natural Area. Data on emergence percents from *G. crinita* seeds sown in 1986 in the Radio Lab field were also relevant. Losses of seeds from the top layer of the soil may be due to seedling emergence, burial to a depth at which emergence cannot occur, or other mortality factors such as seed predation.

The Natural Area

The recording of seedling emergence over two years, from seed sown in fall 1987 in the existing clearings or scrub at the Natural Area is described in detail in Section I of this chapter. Rates of emergence of both *G. crinita* and *D. carota* seedlings declined sharply in the second year (Table 3.1). Percent emergence of *G. crinita* seedlings (from 300 seeds per plot) in individual plots varied from 7 to 38.7% in the clearings, and 13.7 to 52.3% in the scrub, in 1988. In the second year, 1989, relative figures were much lower: 0 to 5.3% in the clearings and 0 to 1% in the scrub. Percent emergence of *D. carota* seedlings varied from 6.7% to 45.3% in the clearings and 1.3 to 20% in the scrub in 1988, while in 1989 rates were 0-6% in the clearings and 0-2.7% in the scrub. As pointed out in Section I, the actual figures are minimum estimates, as plants emerging and dying between censuses would have been missed.

The Radio Lab field

Numbers of seedlings present over three years in plots sown in fall 1986 with 1000 *G. crinita* seeds showed a similar pattern of decline. In five plots located in a part of the field with few flowering *G. crinita* plants and where surrounding unseeded plots had no seedlings, numbers of new seedlings that were present each year (as % of 1000) were: 3.8-16.4% in June 1987, 0.3-3.7% in May 1988 (before the drought), and 0-0.5% in July 1989.

Length of seed dormancy: four greenhouse experiments

Dormancy of seed was investigated by recording: 1) seedling emergence from "fresh" seeds, i.e. emergence in the same year that these seeds were produced; 2) emergence from seeds stratified on Cornell mix for one winter; 3) emergence from seeds that had remained in seed heads on adult plants over one winter; and 4) emergence from seed stored for one year, then given moist stratification.

(1) Seeds were collected from *D. carota* and *G. crinita* plants along the roadside adjacent to the Natural Area in fall 1988. Seeds of each species were sown separately on 23rd November 1988 in 5 pots filled with Cornell mix. Each pot was sown with 25 seeds. Pots were 8 cm by 8 cm and 6 cm deep. The pots were kept in a greenhouse heated to around 15°-20°C and watered as necessary to keep the Cornell mix moist. Seedling emergence was recorded every 1-2 days until 18th December 1988 and once more on 11th January 1989. By 18th December, emergence of *D. carota* seedlings was 20.8% of the 125 seeds sown. Emergence of *G. crinita* seedlings was only 4.8% by this date. By 11th January, emergence of *D. carota* seedlings was 24% and *G. crinita* 14.4%, although this could be an underestimate as seedlings that emerged and died between mid-December and mid-January would have been missed.

(2) A second experiment was set up at the same time and in the same way as described above. However, once the seeds had been sown, the pots were left outside on a flat roof at Cornell University until 28th March 1989, when they were brought into the greenhouse. Seedling emergence was recorded every 3 days until 14th April 1989. Percent emergence for *D. carota* was 50.4% and 57.6% for *G. crinita*.

(3) Seed heads of *D. carota* plants or capsules of *G. crinita* plants can retain some seeds over the winter and into the following spring (see Chapter 4 for more detail). Capsules or seed heads from 4 plants of each species were collected from the Radio Lab field in April 1989. Seed was removed immediately and sown in pots filled with Cornell mix. Four pots per species were set up, one for each plant. Three had 50 seeds and one had 25 seeds. *D. carota* seeds were sown on 3rd April and *G. crinita* seeds were sown on 10th April. The pots were placed in the greenhouse and inspected every 3-4 days. Emergence of *G. crinita* seedlings began on 4th May, and by 31st May percent emergence

was, on average, 18% (range 2 to 34%). No emergence of *D. carota* seedlings had occurred by 31st May.

(4) An experiment to examine seedling emergence in moist versus waterlogged substrates, which is described in detail in Section III of Chapter 5, was set up with seed that had been stored for a year. Seeds of *D. carota* and *G. crinita* were collected in fall 1988 and kept in envelopes, sealed in plastic bags, in a refrigerator at 3°-5°C until October 1989. The seeds were then stratified for 4 weeks by floating them on de-ionized water in the refrigerator. A total of 1000 seeds of each species were sown in pots filled with Cornell mix, on 22nd November 1989. Seedling emergence began on 30th November and was recorded every 3-7 days until 28th December. A very high percentage of emergence was recorded from *G. crinita* seeds in the moist treatment (89.6%), and emergence in the waterlogged treatment was 54.2%. Emergence percents of *D. carota* seedlings were lower: 39.8% in moist conditions and 21.4% in the waterlogged treatment.

Dispersal in space

Introduction

Spatial dispersal of seed is extremely difficult to study directly, particularly seed movement over long distances. Researchers have looked at distribution patterns of species on islands in relation to probable dispersal methods (Carlquist 1967, Gorman 1979) or carried out small scale studies of seed dispersal, for example seed deposition around parent plants (Werner 1975a, Rabinowitz & Rapp 1979).

In an attempt to assess *G. crinita*'s potential dispersal capability, a variety of local scale field experiments and greenhouse studies were carried out. *G. crinita* seeds are relatively small and light (Chapters 2 and 4). They do not have a hard coat and are covered with papery papillae. Their morphology does not seem obviously related to enhancing a particular mode of dispersal, as they are not spiny, unlike *D. carota*, which sometimes may be dispersed by animals (Dale 1974, Gross & Werner 1982), nor do they have a pappus, unlike, for example, seeds of *Tragopogon dubius* (Gross & Werner 1982). However, the hooded papillae may increase buoyancy in air or water. Experiments and observations are reported below on the potential role of two dispersal modes, wind and water, and comments made on the possible role of animal dispersal.

Wind dispersal

Fernald (1950) describes *G. crinita*'s dispersal as follows, "Seeds often all blowing to new areas and the plants disappearing from former stations." This claim was tested by setting up seed traps around parent plants in the field and by estimating potential dispersal distances based on measurements of the terminal velocity of seeds in the laboratory.

Seed traps in the field: methods and results

Seed dispersal in *G. crinita* occurs during late fall and over winter. Most of the seed disperses in the early part of this period (Chapter 4, Fig. 4.2). At the beginning of November 1989, two sets of seed traps were laid out at the Radio Lab field and one set in an old field on Snyder Hill, 8 km to the south. The two Radio Lab sets were located around isolated plants on the edge of the population. The surrounding vegetation was clipped before the traps were installed. At Snyder Hill an individual plant was transplanted from the Radio Lab. The ground was level, and no clipping was required as the vegetation was short. The area had been colonized by pine trees and was more sheltered than the Radio Lab.

The traps were made of white plastic, sprayed with sticky Tanglefoot® and cut to various shapes and sizes. Traps were pegged to the ground with metal spikes. Three layouts were used. At the Radio Lab, one plant (32 cm tall, 9 seed capsules) was surrounded by a complete sheet of plastic 1 m in radius, demarcated into circles of 25, 50, and 75 cm in radius. The other Radio Lab seed trap consisted of 2 adjacent plants (30 cm tall, with a total of 14 seed capsules), surrounded at the base by a 20 cm radius plastic sheet and then by 20 by 20 cm plastic sheets at 0.5, 1, 1.5, and 2 m from the plants, at each of 8 compass points (N, NE, E, etc.). The 48 cm tall plant (with 29 seed capsules) at Snyder Hill had a 50 cm radius plastic sheet around its base, and 20 by 20 cm traps at the 8 compass points, at 1 and 2 m from the plant.

Two weeks after the traps were installed the Snyder Hill set and the 2 m set at the Radio Lab were inspected. Seeds were easily visible on the traps. To try to get an idea of longer term dispersal patterns the 1 m radius trap was left until 13 March 1990 and the seeds counted, by which time the plant had been uprooted (probably by deer).

Numbers of seeds deposited around the plant declined fairly steadily with distance in one set of traps (Fig. 3.10a). In the 1m radius trap, numbers declined with distance from the plant, although there was a second, lower, peak at 75 cm (Fig. 3.10b). In the third trap, numbers peaked around 100 cm from the seed source (Fig. 3.10c).

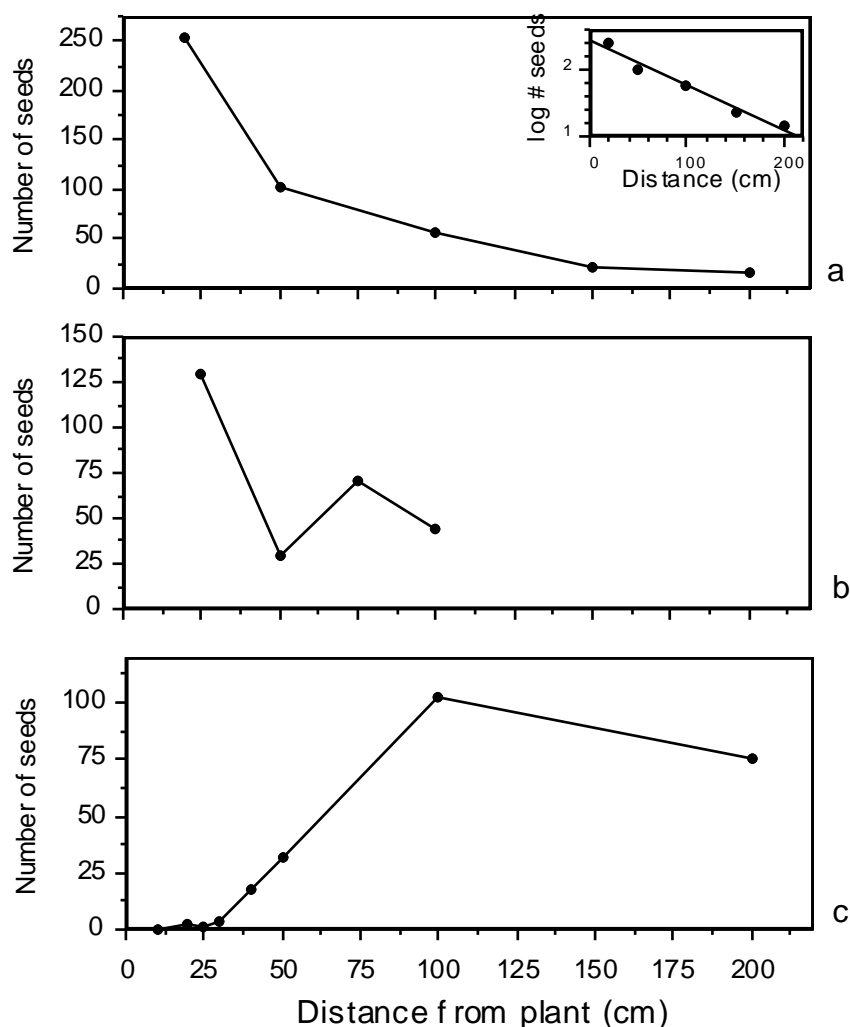


Fig. 3.10. Distribution of seeds around *G. crinita* plants:

a. around 2 plants at the Radio Lab, 15 Nov. 1989 (30 cm high, 14 seed capsules)

Inset: the number of seeds deposited with distance declined exponentially;
 $\log(\text{seeds}) = -.0067 \text{ cm} + 2.4$; $r^2 = .97$.

b. around 1 plant at the Radio Lab, 13 March 1990 (32 cm high, 9 seed capsules)

c. around 1 plant at Snyder Hill, 15 Nov. 1989 (48 cm high, 29 seed capsules).

The seed trap in (b) was 1 m in radius; all seeds found at each distance are shown. The others (a and c) included 20 by 20 cm traps at 8 points of the compass, so the total number of seeds estimated to have fallen at each distance as shown is based on the area of traps relative to the increasing area available in zones at increasing distance around the central seed source.

Calculation of terminal velocity in the laboratory: methods and results

In November 1989, a laboratory experiment was carried out by Dr. Karl Niklas (Cornell) and myself to calculate the terminal velocity of fresh *G. crinita* seeds when they fall through the air. The result was then used to determine the potential distances that seeds might travel at different wind speeds, as the slower a seed falls, due to mass and aerodynamic form, the farther it will travel at a given wind speed.

Seeds were dropped into a jar under stroboscopic light which was set at a known frequency of cycles per minute. As the seeds fell they were photographed, and the resulting prints showed the repeated images of individual seeds falling through the air. When the terminal velocity was reached, the distance between these images became constant. By measuring this distance and using the known time lapse between images (from the frequency of the stroboscope) the terminal velocity in m/sec was calculated. The experiment was repeated several times and the clearest images used.

The results showed a little variation as some seeds were lighter than others. Therefore the minimum, median, and maximum velocities were used to plot potential dispersal distances (Fig. 3.11). Potential dispersal distance was calculated, assuming no turbulence, by multiplying wind speed (m/sec) and height of capsule above the ground (release height) and dividing by terminal velocity of the seed (m/sec). Under most wind conditions at Ithaca, the potential dispersal distance was less than 4 meters for release heights of 50 cm or less. Occasionally, *G. crinita* plants over 50 cm in height were seen during the project, but most were smaller. The median height of flowering *G. crinita* at the Radio Lab field was less than 25 cm between 1987 and 1989, and none were over 50 cm (Chapter 4). In 31 localities in New York State, median height was less than 35 cm in 1989 (Section I of Chapter 5) and three-quarters of all plants were less than 50 cm in height.

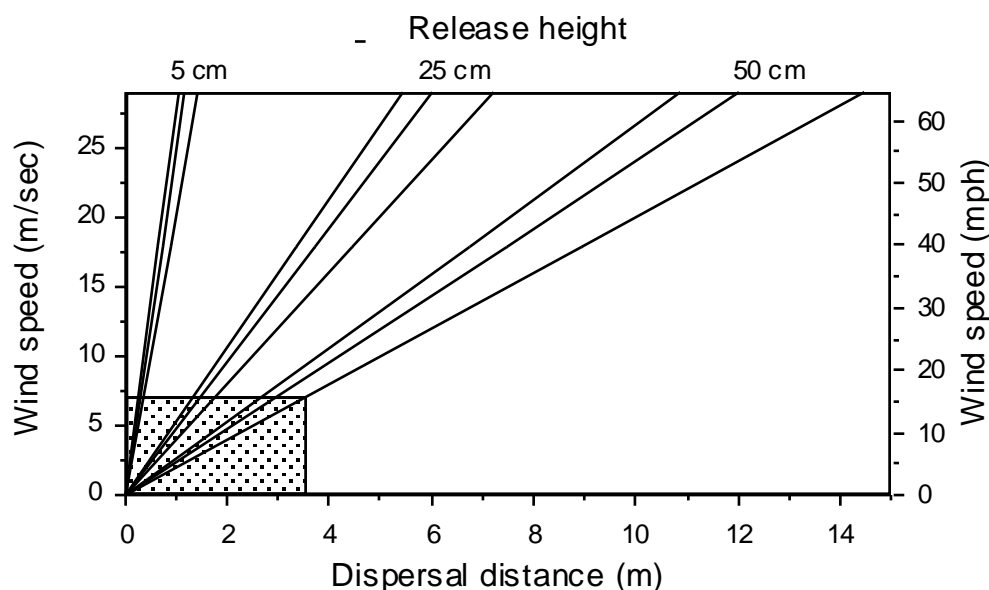


Fig. 3.11. Potential dispersal distances based on the terminal velocity of *G. crinita* seeds (minimum of 1.0 m/sec, median 1.2, maximum 1.3) at three release heights. The shaded area represents 97% of the recorded hours of average wind speeds at the Game Farm Road, Ithaca, weather station from 1983-1988 (Dr. K. Eggleston, Northeast Regional Climate Center, Cornell, pers. comm.), which were ≤ 7.15 m/sec (16 mph). Maximum gusts recorded each month at Syracuse Airport, New York, were 23.2 to 27.3 m/sec (52-61 mph) between November and April in 1988 (Eggleston, pers. comm.).

Dispersal by water

G. crinita and *D. carota* seeds float in water, so the potential for dispersal by this method was investigated by studying the emergence of seedlings from seeds subjected to different amounts of time floating on water. Although it is quite difficult to destroy the buoyancy of *G. crinita* seeds (they have to be vigorously shaken in a closed test tube before they sink), they may become trapped below the water surface during the process of dispersal. To test whether seeds would still be viable after such immersion, emergence of seedlings from *D. carota* and *G. crinita* seeds that had been totally immersed was also studied.

In addition to these two experiments, a small experiment was carried out to test the effect of ground cover on movement of *G. crinita* seeds in overland flow of water. Given the buoyancy of *G. crinita* seeds, they might easily travel some distance over the ground in flood conditions, particularly where the land is sloping, and they may be subsequently washed into streams and rivers. At the Letchworth site, overland flow of water became rapidly apparent during heavy rain (pers. obs.). However, distance travelled by seeds may partly depend on the type of ground cover. The strong association of *G. crinita* seedlings with moss, as noted in Section II of this chapter, may result from seeds becoming trapped in the moss, and so this was studied in the laboratory.

Experiments in the laboratory and greenhouse: methods and results

(1) In the fall of 1988, seeds of *G. crinita* and *D. carota*, collected from the roadside adjacent to the Natural Area, were floated on distilled water in separate petri dishes for different periods of time. The dishes were kept in a refrigerator during these periods and then the seeds were planted in Cornell mix and overwintered on a flat roof at Cornell. Five replicates of 25 seeds per dish were subjected to floating periods of one hour, one day, one week, or one month. Five replicates were planted without pretreatment. The pots were brought into the greenhouse on 15 March 1989. Emergence began on 28 March and was recorded every 3 days until 14 April.

Neither species showed significant differences in emergence among treatments (Kruskal-Wallis tests of % emergence per pot, within species; $p > .05$). Mean emergence was similar; 62.2% (± 4.2 , s.e.) for *G. crinita* and 57.9% (± 2.2) for *D. carota*.

(2) In the fall of 1989, *G. crinita* and *D. carota* seeds, collected in fall 1988, were immersed in distilled water by trapping them between 2 layers of filter paper at the bottom of petri dishes. For each species (separately) 50 seeds were immersed in each of 9 dishes, and 50 were floated in each of another 9 dishes. The dishes were kept in a refrigerator for 17 days and then the seeds were planted in Cornell mix and moved to the greenhouse on 6 December. Emergence began on 15 December and was recorded until 26 December.

No difference in emergence between floated and flooded treatments was found (Mann-Whitney tests, $p > .05$) although emergence of *D. carota* was much lower than *G. crinita* in both treatments perhaps due to loss of seed viability during storage from 1988 to 1989 (flooded treatment 69.2% for *G. crinita*, 9.1% for *D. carota*; floated treatment 67.5% for *G. crinita*, 14.0% for *D. carota*).

(3) In the fall of 1989 a small test of the ability of moss to trap *G. crinita* seeds was carried out in the laboratory. *G. crinita* appeared to be particularly associated with the presence of moss at Letchworth. An acrocarpous, tufted moss from greenhouse pots (probably *Funaria* sp., F.R. Wesley, pers. comm.) was used for the experiment. The three mosses growing in the transects at Letchworth, and identified by Dr. Pat Martin (see Chapter 2), were also acrocarpous species. Moss from the greenhouse was put into 2 petri dishes with enough soil so that it was above the rim of the dish. Fifty seeds were put into the center of each dish, dishes were immersed in water to a depth of 4-5 cm, and the seeds that floated off were counted. Then the dishes were removed, held at about a 30° angle, and

approximately 200 ml of water poured over them twice. Any additional seeds that were washed off were counted after each washing. The results were as follows:

	<u>Lost by flooding</u>	<u>Lost by first washing</u>	<u>Lost by second washing</u>
Dish 1	30	8	0
Dish 2	37	3	0

The percentage trapped by the moss was therefore 24% and 20% respectively.

Animal dispersal

No direct observations were made on the role of animal dispersal. Unlike *D. carota*, *G. crinita* seeds have no spines or barbs that would enhance animal dispersal. However, in common with many other species that appear to have no special means of dispersal, they might be transported in mud on animals' feet (Fenner 1985). In some sites populations did seem to be associated with the edges of deer trails (pers. obs.). Perhaps the depredations of deer on flowers and seed capsules may also lead indirectly to some dispersal of seed.

Discussion

Dispersal in time

The results from the scrub clearance experiments at the Natural Area, and data on decline in rates of emergence and on length of dormancy of seeds, suggest that *G. crinita* does not have a substantial persistent seed bank that can respond to the intermittent appearance of forest gaps. The three plants that appeared in the large cleared plots may either have come from a limited, relatively short-lived, seed bank derived from the small, declining population of recent years, or from a few seeds that have survived from times when population numbers were high. In either case, disturbance leading to the removal of tall scrub cover in a locality like the Natural Area would have to be frequent, say every 10 years or less, for *G. crinita* to have much chance of appearing in sufficient numbers to survive hazards such as deer damage, and re-establish a population from a buried seed bank. The poor response by *G. crinita* to the efforts made in the 1970's and mid 1980's to clear areas in the southern part of the Natural Area, where populations were probably rather low even before the scrub grew up, may therefore be due to lack of any sizeable, long term seed bank. *G. crinita* can survive and reproduce in these clearings if seed is introduced, as shown in Section I.

The emergence percents recorded in the field and greenhouse suggest that more seeds germinate in the first growing season after dispersal than in following years, even if they are in unfavorable habitats like the scrub where future survival is unlikely (Section III of this chapter). A similar response to unfavorable conditions was noted during an experiment to assess emergence and survival in three soil types (Section III of Chapter 5). In this experiment, emergence of *G. crinita* was not inhibited by acid soil compared to emergence in mildly acidic or calcareous soil. However survival in the acid soil was much lower than in the other two soils. *G. crinita*'s behavior is paralleled by that of *Gentianella germanica* in chalk grassland (Schenkeveld & Verkaar 1984). Germination of seeds of this species is not inhibited by dense turf, but the seedlings do not survive there.

In contrast, fewer *D. carota* seedlings emerged in acid soil or under scrub compared to more favorable conditions (Section I of this chapter, and Section III of Chapter 5). Perhaps *D. carota* responds to more precise germination cues and remains dormant if these cues are absent. Leaf canopy-induced dormancy, which has been found in *D. carota* (Silvertown 1980), may not be significant as both species disperse at a time when the canopy is dying back or has disappeared. In the case of seedling emergence under scrub (Section I of this chapter) most seedlings of both species emerged before the canopy leafed out (pers. obs.).

Emergence rates from an initial seed crop decline with time in many species (Roberts & Feast 1972, Werner 1977, Baskin & Baskin 1986) including *D. carota* (Holt 1972, Lacey 1978, and my study). Disturbance may increase emergence compared to undisturbed conditions, but numbers still decline (Roberts 1986) although at different rates for different species (Cook 1980).

In Warwickshire, England, Roberts (1986) found that percent emergence of *D. carota* seedlings from seeds collected and sown that year was only 2%. Most seedlings emerged in the year following the one in which seeds were sown. The seeds had been sown in sandy clay loam in cylinders 30 cm long, sunk in the ground outdoors. Each year the soil in the cylinders was disturbed three times, and after 5 years emergence had declined to 0.3%. Lacey (1978) reported that buried *D. carota* seeds remained viable for up to 5 years, but seeds kept out of the soil or on its surface declined in viability. This result fits with my findings of reduced viability of *D. carota* after storage, and lack of germination by seeds remaining on the plant over winter.

The results of the greenhouse experiments on dormancy suggest that the majority of *G. crinita* and *D. carota* seeds are not ready to germinate without an "after-ripening," dormant period, over the winter following fall seed production. The results for *D. carota* were similar to those obtained by Roberts (1986), described in the preceding paragraph. Most seeds have been dispersed by the spring (see Chapter 4) and probably undergo cold, moist stratification in contact with the soil. Some *G. crinita* seeds can still germinate in spring even if they do not have stratification in the soil, unlike *D. carota* seeds. In contrast to *D. carota*, enforced, artificial delay of *G. crinita* germination, by storing them dry in a refrigerator for a year and then giving them cold, wet stratification, merely increased emergence. Thus some *G. crinita* seeds may take more than one winter to after-ripen, but most of these are probably ready to emerge under field conditions after two winters.

In undisturbed vegetation the seeds may become buried by litter and humus development. As Lacey (1978) pointed out, seeds of *D. carota* may remain viable over the longer term only if they are buried. However, without any disturbance, as time passes it seems likely that fewer seedlings of either species would be able to emerge successfully, particularly the tiny *G. crinita* seedlings. Farmer (1978) showed that *G. crinita* seeds could germinate in the dark after cold, moist stratification. However, the seedlings, being so small and of rosette form, are unlikely to be able to reach the surface from any depth greater than a few millimeters. The greater emergence of *G. crinita* seedlings in the 'heavy disturbance' treatment in the Natural Area (Section I of this chapter) compared to the other treatments may have been due to lower litter amounts. Litter was totally removed by the treatment and may have taken some time to build up again, so more seeds escaped burial during 1988-89. At Letchworth, where there is considerable bare ground and soil movement, *G. crinita* seedlings emerged throughout the transects in 1988 even though only one flowering individual was present in 1987. Thus the seedlings probably derived from seed shed in 1986 or previous years. A comparison of emergence rate under controlled conditions of disturbance versus no disturbance and an assessment of the viability of remaining seed would help elucidate the relationship of *G. crinita* to disturbance.

G. crinita's probable lack of a long term seed bank is not unusual. It seems that *D. carota* also lacks a persistent seed bank. This lasts about as long as *G. crinita*'s seed bank, i.e. several years (Dale 1974, Lacey 1978, Roberts 1986), rather than just the one or two years mentioned by Gross and Werner (1982).

Grubb (1976) outlined two main strategies for annuals and biennials of open habitats in forest zones. Some species, like *D. carota*, exist in the "predictable" open sites such as cliffs, edges of marshes, or sand dunes, and produce rather low numbers of seeds, with little dormancy. Other species exploit "unpredictable" short-lived sites such as forest clearings, through large seed output and/or specialized dispersal mechanisms and long seed dormancy. Grubb classified *Gentianella amarella*, *G. anglica*,

and *G. germanica*, along with *D. carota*, as species of "predictable" open habitats. He considered that these *Gentianella* species may have some short-term dormancy but may not persist over many years, as I found for *G. crinita* seeds. De Jong et al. (1987) found that 50% of biennial species, in data collected by Ødum, did not accumulate seeds in the soil. However, plants typical of woodland clearings, which Grubb called "unpredictable" habitats, such as *Digitalis purpurea*, *Verbascum thapsus*, and *Oenothera biennis* did have persistent seed banks. The issue of relative seed output of *G. crinita* and *D. carota* is examined further in Chapter 4.

To summarize, *G. crinita* fits Grubb's category of species typical of "predictable" open habitats in terms of its seed bank, and requires that these habitats remain unforested if a population is going to persist in a locality without immigration of seed from elsewhere. However, common species including *D. carota* also fall into this category, so other factors seem to be of greater significance in limiting *G. crinita*'s distribution and abundance.

Dispersal in space

By spring, a very small proportion of the seeds from the previous fall remain in the seed capsules of *G. crinita* (Chapter 4). Contrary to Fernald's (1950) statement about wind dispersal, the evidence from the seed traps and estimation of terminal velocity suggests that most of these seeds fall quite near the parent plant. This behavior is found widely in other species (Cook 1980, Werner 1975a). The peaks in numbers a little distance from the parent plant, seen in two of the traps, are also characteristic of many other species (Harper 1977, Okubo & Levin 1989). Okubo and Levin (1989) identified mean wind speed, height of release, settling velocity of seeds, and turbulence as important factors in models of these dispersal distributions. A peak at 75 cm from the *G. crinita* plant in the 1 m radius trap was partly due to a group of seeds that dispersed together for some reason (perhaps held together by a thread of a seed-eating Lepidoptera larva, Chapter 4). Another possible cause of peaks that occur away from the seed source (e.g. Fig. 3.10c) may be a requirement for the wind to be above a certain "threshold" speed, which would shake the rather rigid stem and capsule sufficiently to release the seeds, and disperse them a little distance from the plant. The graph of potential dispersal distances (Fig. 3.11) shows that even the strongest gusts would not move the seeds very far. Turbulence might increase distances but not significantly, because the seeds fall relatively fast (Dr. K. Niklas, pers. comm.). Okubo and Levin (1989) regard seeds that fall at velocities of > 1 m per second (which would include *G. crinita* seeds) as "heavy" and turbulence insignificant in models of dispersal distributions of these seeds.

Wind dispersal over snow and ice is a factor to consider, as the seeds disperse over the winter. Lacey (1982) studied the dispersal of 300 loose *D. carota* seeds placed in a terminal umbel on a plant located on a lawn in Michigan. After one hour she found that average dispersal distances for *D. carota* in a 16 mph wind (7 m/sec) were 2.5 ± 1.2 m (std. dev.) and no seeds travelled more than 6.25 m. However, when 300 seeds were placed on snow, 12% of seeds were found to have moved 16 m downwind, in winds of 15-25 mph (7-11 m/sec). Lacey noted that suitable conditions, i.e. crusty snow and strong winds, only occurred two or three times in a winter season. Dispersal over snow by *G. crinita* seeds might be possible from the tallest plants. Small ones a few centimeters high are likely to be covered by snow, while other individuals are often much the same height as surrounding vegetation, which could hamper dispersal. Infrequency of suitable conditions and interference from other plants probably preclude much long distance dispersal by *G. crinita* over snow.

G. crinita seeds were not damaged by floating in water, indeed that treatment proved a very effective stratification technique. Giersbach (1937) also found moist stratification at 1° or 5°C for 1 to 4 months was effective, whereas very poor germination resulted if seed was put straight into the greenhouse and kept in temperatures between 15° and 30°C. Dispersal by cold winter snow melt or floodwater therefore seems ideal. If seeds are not trapped, for instance by moss cover, and can reach streams, movement over quite considerable distances in a river system might be possible.

The role of animal dispersal deserves greater attention, including the effect of human activities. For instance, *D. carota* was one of many species that germinated from mud collected underneath a car in an experiment by Schmidt (1989). Machine mowers may have spread *G. crinita* locally along roadsides around the Radio Lab area in Tompkins County. Its ability to survive in pastures and meadows and on roadsides would seem to give it similar chances to be dispersed by humans and domestic stock as, for example, *D. carota*, though perhaps it is less likely to be transported on clothing or animal fur. Lacey (1978) found that *D. carota* seeds adhered to fur of raccoon and skunk but not rabbits and mice.

Overall, *D. carota* seems to have considerable ability to spread rapidly over long distances. It was introduced into North America from Eurasia probably not more than 300-400 years ago. Its first recorded presence in North America was in 1739 (Dale 1974). Yet its distribution now extends beyond *G. crinita*'s range. It was present in all except 4 of the 32 sites in my survey of New York State localities that had *G. crinita* (Section I of Chapter 5), and *D. carota* had occurred in 2 of those 4 sites in the past (G. Chase, pers. comm.).

G. crinita does not appear to have significantly lower potential for spatial dispersal, although it has no obvious characteristics that would aid animal dispersal. However, other biennials, such as *Verbascum thapsus*, also lack these characteristics. Introduced *Verbascum thapsus* has spread rapidly across much of North America and is very common in some localities (Reinartz 1984, Gross & Werner 1982). Therefore, to summarize, *G. crinita* does not appear to be scarce because of any obvious lack of ability to disperse over long distances.

CHAPTER 4

REPRODUCTIVE PERFORMANCE OF *Gentianopsis crinita*

INTRODUCTION

Reproductive performance is one of the principal life history characteristics of biennials to have attracted attention from ecologists (for example, Grubb 1976, Hart 1977, Spira & Pollack 1986, Kelly 1989a). Biennials are monocarpic, i.e. limited to a single reproductive event after which the adult plants die. They do not reproduce by vegetative means and can only reproduce by developing and dispersing seeds. Several ecologists have suggested that if biennials are to be successful they need to have a high reproductive output to compensate either for the delay in flowering compared to annual plants or for the repeated production of offspring by polycarpic perennials (Harper 1977, Hart 1977, Silvertown 1983, Thompson 1984).

The rare biennial, *Gentianopsis crinita*, may be critically limited in its abundance by poor performance during the reproductive phase of its life cycle. This chapter will examine the hypothesis that the relative scarcity of *G. crinita* is due to the low reproductive output of adult plants compared to the common biennial, *Daucus carota*. Over the period 1987 to 1989, the reproductive output of the two species, in the form of flowers and seeds, was compared in established populations in New York State. The study included assessing the relative significance of various causes of pre-dispersal losses of seeds. The specific questions addressed were as follows:

1. Did *G. crinita* produce fewer flowers compared to the number of umbels produced by *D. carota*?
2. Were there fewer seeds in *G. crinita* flowers than in *D. carota* umbels?
3. Did *G. crinita* suffer greater pre-dispersal losses of flower heads and seeds than *D. carota*?
4. Did the species differ in frequency of flowering events?

METHODS

Most of the work was carried out at the Radio Lab site near Ithaca, but some recording was done in the Natural Area near Ithaca, and in Letchworth State Park.

Production and loss of flowers, fruits and seed capsules

To assess the relative production of flowers, fruits and seed heads by plants in the established populations of *G. crinita* and *D. carota* at the Radio Lab field, randomly selected individuals of each species were marked on dates between late July and mid-August (30th July - 17th August) each year from 1987 to 1989. The plants that were marked had elongated central stems and were thus entering or were already within the reproductive phase of their life cycle as described in Chapter 2. Sixty plants of each species were marked in 1987, 40 of each in 1988 and again in 1989. The numbers of reproductive heads on each plant were counted, i.e. buds, flowers, fruits, seed capsules for *G. crinita* or flower umbels that then developed into seed heads for *D. carota*. Plants were censused and counts of reproductive heads were repeated in early to mid-September (6th-19th), mid-October (9th-18th), and the end of November to early December (25th November - 2nd December). An additional count was made on 6th November 1989, in between the October and late November census. Observations at the Radio Lab field during the winter and early spring months of 1988 indicated that the senesced remains of the adult plants persisted over the winter, and some still had recognizable seed capsules or seed heads in the early spring. Therefore the plants marked in 1988 and 1989

were censused in snow-free periods into the following spring. Data were collected on 13th January, 15th April, and 23rd May in 1989, and 25th January, 13th March, and 24th April in 1990.

From August to late November or early December, the condition of the reproductive heads on each plant was recorded, except for *D. carota* in August 1988. The categories of condition for *G. crinita* heads were (1) undamaged, (2) partially eaten or chewed by mammals or invertebrates, (3) shrivelled, and (4) head nipped off but flower stem still present. These flower stems appeared to have been bitten through, usually diagonally across the stem, suggesting that deer were probably responsible (D. Bassett, Letchworth State Park Naturalist; pers. comm.).

Flower umbels of *D. carota* rarely showed signs of being bitten off, but frequently shrivelled umbels appeared to have broken off before seed developed. These umbels were observed to have narrowed shrivelled stems immediately below the base of the umbel, and where the umbels had been lost the stems tapered to a fine point. The reproductive heads (umbels) of *D. carota* were therefore assigned to the following categories: (1) undamaged, (2) partially eaten or chewed, (3) heads shrivelled or broken off, and (4) heads nipped off. By January the plants and remains of damaged heads of both species were all very shrivelled, so categorization of condition was not attempted. However, undamaged heads remained easily recognizable.

Observations made on second-year *G. crinita* plants in 1986 and 1987 at the Radio Lab field and along the roadside adjacent to the Natural Area indicated that plants that had lost the top of their central stem, due to mammal, insect or mowing damage, could subsequently produce new side shoots that later bore flowers. To try to quantify the impact of loss of stem-tops on reproductive output, the occurrence of such damage was noted in August and September each year for the marked plants. The numbers of reproductive heads produced by undamaged and damaged plants could then be compared.

Seed dispersal

The pattern of seed dispersal over time was recorded by estimating by eye the proportion of seed remaining in capsules (*G. crinita*) or seed heads (*D. carota*) at census dates. The estimates were expressed as percentages, to the nearest 5%. The estimates were considered to be reasonably accurate, although it would have been worth making independent tests of actual proportions of seed remaining (i.e. numbers left), compared to estimated percentages. The average for individual plants was obtained by averaging the percentages for all the capsules or seed heads on the plant.

Estimation of relative reproductive output

The records of numbers of reproductive heads and the amount of seed dispersal at different dates were considered to give reasonable and practical estimates of the relative reproductive output of the two species. Marking of individual reproductive heads and intensive re-recording would have given better absolute figures but would have been difficult to pursue once snowfall began, as happened usually in November. Thereafter part or all of some plants as well as the markers were covered by snow for considerable periods.

Seed numbers and weights

To assess the relative numbers of seeds per capsule or head, a separate random sample of plants was identified at the Radio Lab field each year from 1987 to 1989 and a capsule or head collected from each plant. The collections were made as seeds were ripening but before much seed had been dispersed by plants in the population as a whole. Capsules or heads chosen for collection appeared to have ripe but undispersed seed. One capsule or head was collected from each plant, chosen at random if more than one capsule or head satisfied the requirements for ripe and undispersed seed.

D. carota heads were collected in mid-October (11-16th) and *G. crinita* capsules on dates from the end of October to mid-November (28th October - 16th November).

In 1988 and 1989 a similar collection of seed heads and capsules was made at the Letchworth study site. Plants were randomly selected from 10 m by 10 m areas on either side of the transects (described in Chapter 2). *D. carota* was collected on 4th October 1988 and 1st October 1989 and *G. crinita* on 4th November 1988 and 30th October 1989.

The seeds in each capsule or head were assigned to two categories: filled and unfilled. Unfilled seeds were recognized by their flat shape. The numbers of seeds in each category were counted. In 1989 the filled seeds from each head or capsule were weighed. The average weight of a seed from that capsule or head was obtained by dividing the weight by the number of filled seeds in each capsule or head. All *G. crinita* seeds collected were returned to their site of origin after counting and weighing were complete.

Timing of reproductive events

Data from other experiments and observations carried out at the study sites provided information on the timing of reproductive events. *G. crinita* and *D. carota* seedlings were marked in the transects at Letchworth State Park in 1987 as part of a study on regeneration in different microhabitats (Chapter 3, Section II). In 1988 and 1989 the numbers of surviving plants that entered the reproductive phase were recorded. Reproduction among plants marked for a similar microhabitat study in the Radio Lab field in 1987 and 1988 was also recorded in 1988 and 1989. A study in the Natural Area of the establishment, survival and reproductive output of plants in different successional stages of vegetation (Chapter 3, Section I) provided additional information on the timing of reproduction.

Data analysis

Differences in reproductive output were generally analyzed using non-parametric tests as the data were often not normally distributed. For this reason medians rather than means are quoted in the results.

RESULTS

Production and loss of flowers, fruits and seed capsules

The total numbers of reproductive heads recorded from the sample plants of both species showed a similar pattern of change through time from August to December each year (Fig. 4.1). The total numbers at each census date included all visible reproductive heads or their remains such as flower stems but were not "absolute" figures, as they did not include heads which appeared and disappeared between census dates. Numbers of heads increased from August to September for both species as new heads developed, and then numbers declined at later dates as losses accumulated, although the peak and decline in numbers of *D. carota* umbels were not as marked as for *G. crinita* (Fig. 4.1). The peak for *G. crinita* was delayed until October in 1988, probably because the drought which affected the area earlier in the season (see Chapter 2) slowed the growth and development of second-year plants.

The overall totals of reproductive heads of *G. crinita* at each census date were always greater than totals of *D. carota* heads (i.e. umbels) even in the drought year of 1988 although the difference was less marked (Fig. 4.1). This difference between *G. crinita* and *D. carota* was confirmed when the total number of heads per plant for each species was compared for September each year. The figures analyzed represent estimates of the maximum relative numbers of total heads per plant in September, as plants which had not yet developed any heads (particularly the case for *G. crinita* in

1988), and those few which had none at all owing to damage, were excluded. As can be seen from Table 4.1, the differences were highly significant for 1987 and 1989. As found for the overall totals of reproductive heads, although *G. crinita* had more heads per plant than *D. carota* in September 1988 the difference was less marked.

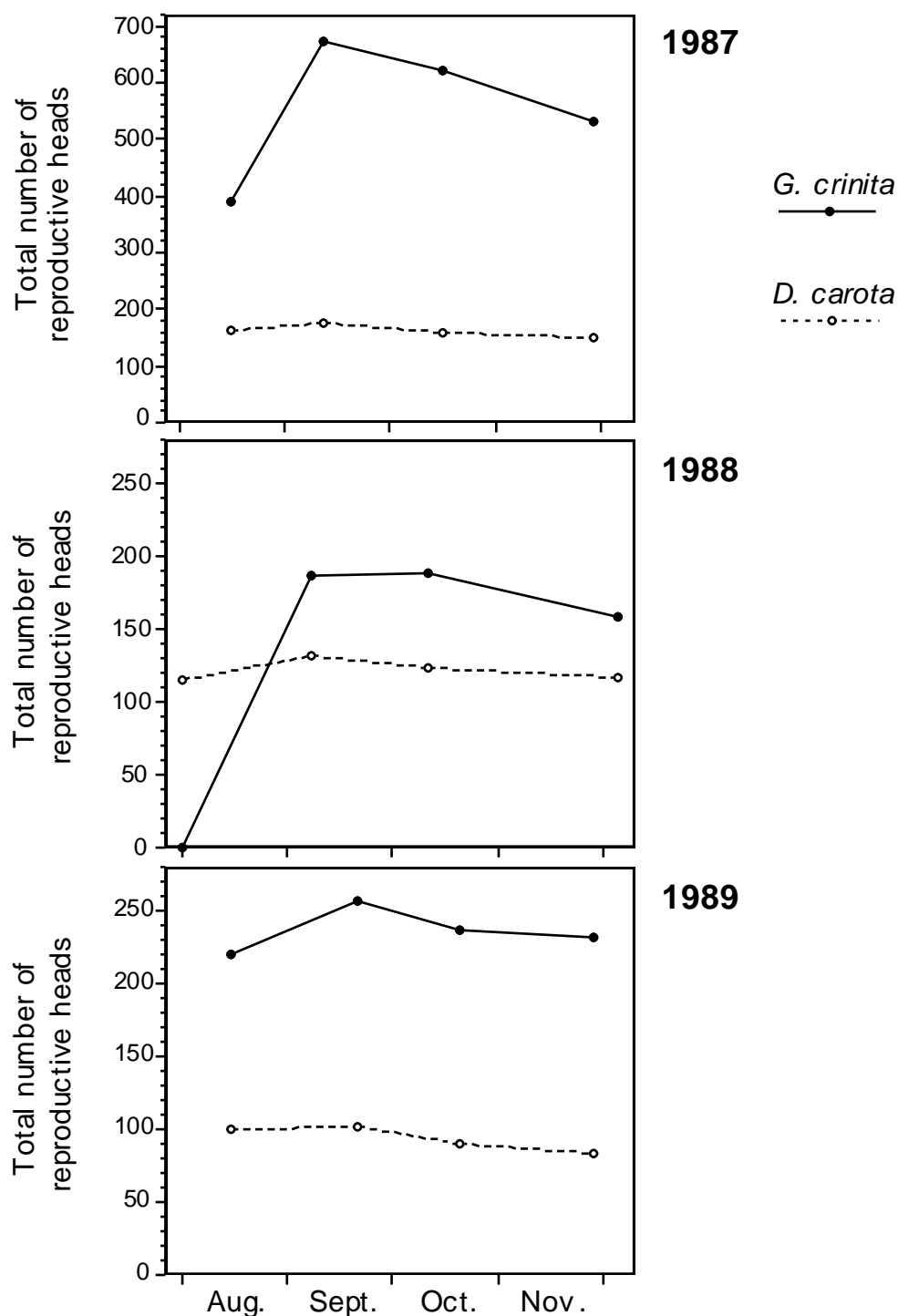


Fig. 4.1. Pattern of reproductive output of *G. crinita* and *D. carota* in the Radio Lab field, measured by total number of reproductive heads (seed capsules or umbels) recorded for each sample. For 1987 $n = 60$ plants of *D. carota* and 55 of *G. crinita* as there were 5 missing values in November that year. For 1988 and 1989 $n = 40$ of each species. Note that 1987 is shown on a different scale.

Table 4.1. Numbers of reproductive heads per plant, numbers of seeds per head, and average weight of seed for *D. carota* and *G. crinita* at the Radio Lab field in 1987-1989. Reproductive head for *G. crinita* (Gc) refers to the flower or the seed capsule; for *D. carota* (Dc) it is the umbel. The two species were compared with Mann-Whitney U tests. Seed numbers and weights were derived from a separate sample from that used to calculate numbers of heads per plant.

Year	<i>D. carota</i>			<i>G. crinita</i>			Difference	p value
	n	Median	(Range)	n	Median	(Range)		
<u>Total numbers of reproductive heads per plant in September</u> (excluding plants with no reproductive heads at this date)								
1987	60	3	(1-9)	58	9.5	(1-39)	Gc > Dc	.00001
1988	37	3	(1-7)	31	6	(1-15)	Gc > Dc	.005
1989	40	2	(1-7)	40	5	(1-16)	Gc > Dc	.00001
<u>Numbers of undamaged heads per plant in October</u>								
1987	60	1	(0-5)	60	5	(0-25)	Gc > Dc	.00001
1988	40	1	(0-5)	40	2	(0-12)	Gc > Dc	.047
1989	40	1	(0-5)	40	4	(0-13)	Gc > Dc	.0002
<u>Numbers of heads per plant that had dispersed >90% of seed by April</u>								
1988	40	1	(0-5)	40	1	(0-7)	ns	
1989	40	1	(0-5)	40	2	(0-12)	Gc > Dc	.048
<u>Total numbers of seeds per head</u>								
1987	40	116.5	(4-377)	33	289	(61-629)	Gc > Dc	.00001
1988	40	149.5	(23-437)	37	437	(103-882)	Gc > Dc	.00001
1989	40	104.5	(13-301)	57	369	(24-1156)	Gc > Dc	.00001
<u>Numbers of filled seeds per head</u>								
1987	40	103	(2-314)	33	255	(56-612)	Gc > Dc	.00001
1988	40	96.5	(0-339)	37	437	(98-882)	Gc > Dc	.00001
1989	40	88	(2-242)	57	366	(21-1120)	Gc > Dc	.00001
<u>Average seed weight (mg)</u>								
1989	21	0.612	(0.311-1.853)	28	0.066	(0.046-0.097)	Dc > Gc	.00001

The drought may have reduced *G. crinita*'s production of flowers in 1989 as well. In September 1987 plants had more heads than in 1988 or 1989 (Kruskal-Wallis test, $H = 13.11$, multiple comparisons as in Conover 1980, $p < .05$), and there was no difference between 1988 and 1989. This pattern might be expected if the drought also reduced growth of first-year plants in 1988 and this reduction was then carried over into flower production the following year. This relationship between size of first-year

plants and flower numbers the following year is described in more detail in Chapter 5, Section II. In contrast to the behavior of *G. crinita*, *D. carota* plants produced more flowers in the drought year than in 1987 or 1989 (Kruskal-Wallis $H = 12.24$, multiple comparisons, $p < .05$) and numbers in 1987 and 1989 were not significantly different.

The decline in the total number of reproductive heads of both species from the September or October peak represented heads which simply disappeared without trace, either because herbivory completely removed the evidence or the heads became unrecognizable as the whole plant senesced. This may have been particularly the case in 1987 for large *G. crinita* plants that had many flowers, including small buds or flowers low down on the stem. Sometimes these apparently did not develop further but had vanished among the mass of shrivelled leaves on the stem by the next census date.

To assess the relative importance of visible causes of loss of reproductive heads, the data on proportions of heads in the different categories of damage were examined for the October census date. At this time each year the initial cause of loss or damage was most clearly evident. In September relatively few heads had been lost or damaged (<30% of *D. carota* heads and <15% of *G. crinita* heads over the three years). By the end of November many plants had senesced, making it more difficult to identify individual heads, and some could have changed categories, for instance a partially eaten capsule could subsequently shrivel or be nipped off.

Comparisons between species were made using the numbers and proportions per plant for each sample, and the mean ranks were compared using Mann-Whitney tests. Every year in October, *G. crinita* had greater numbers of undamaged heads remaining per plant than *D. carota*, although the difference was not so marked in 1988 (Table 4.1).

Of those plants which still had reproductive heads, the proportion of undamaged *G. crinita* heads per plant was greater than that for *D. carota* in 1987 and 1988 but was not different in 1989 (Table 4.2). A very low proportion of *D. carota* heads appeared to suffer from mammal or insect damage, but many umbels shrivelled before seed was set. In contrast, a lower proportion of *G. crinita* heads were shrivelled, but the proportion that had been nipped off or partially eaten was generally greater (Table 4.2). The actual proportion that shrivelled may have been somewhat underestimated for *G. crinita*, especially in 1987, if unknown losses were really because heads shrivelled and became unrecognizable (as described above). The reasons that buds or flower heads shrivelled were usually not evident. Sometimes Lepidoptera larvae were found on shrivelled buds and leaves at the top of *G. crinita* plants, and their possible effect on subsequent flower production is described below.

Table 4.2. Proportions of reproductive heads of *G. crinita* and *D. carota* in different categories of loss or damage at the Radio Lab field in 1987-1989. Reproductive head for *G. crinita* (Gc) refers to the flower or the seed capsule; for *D. carota* (Dc) it is the umbel. Percentages are relative to the total number of heads sampled: for *G. crinita*, 684 heads in 1987, 189 in 1988, and 236 in 1989; for *D. carota*, 158 heads in 1987, 124 in 1988, 90 in 1989. For each category, the Mann-Whitney U was used to test the difference between the two species in the proportion of the heads on each plant that were affected.

	<u>D. carota</u>		<u>G. crinita</u>		Difference in per-plant proportions	p value
Year	Number	%	Number	%		
<u>Undamaged heads</u>						
1987	73	46.2	359	52.5	Gc > Dc	.02
1988	50	40.3	113	59.8	Gc > Dc	.002
1989	62	68.9	177	75.0	ns	
<u>Heads shrivelled and broken off (D. carota) or shrivelled (G. crinita)</u>						
1987	79	50.0	126	18.4	Dc > Gc	.00001
1988	72	58.1	23	12.2	Dc > Gc	.00001
1989	28	31.1	41	25.8	Dc > Gc	.006
<u>Heads nipped off</u>						
1987	6	3.8	84	26.9	Gc > Dc	.00001
1988	2	1.6	25	13.2	Gc > Dc	.02
1989	0	0	45	19.1	Gc > Dc	.003
<u>Heads partially eaten or chewed</u>						
1987	0	0	15	2.2	Gc > Dc	.001
1988	0	0	28	14.8	Gc > Dc	.00001
1989	0	0	1	0.4	ns	

More *G. crinita* plants than *D. carota* plants failed to produce any seed heads, although the differences were not significant in 1987 and 1988 (Table 4.3). Sample sizes were small and so data on types of damage were pooled for all years. The results parallel those for damage to flower heads, as a higher proportion of *G. crinita* plants out of the total were eaten off compared to *D. carota* ($\chi^2 = 8.02$, $p = .005$). However, among the plants that produced no heads, the differences between the two species with regard to numbers of plants eaten off and numbers suffering other types of damage were not significant (χ^2 tests, $p > .05$).

Table 4.3. *G. crinita* and *D. carota* plants which bolted but did not produce any seed heads.

(a) Numbers of *G. crinita* and *D. carota* plants which did not produce seed heads (capsules or umbels) in the Radio Lab field in 1987-1989. Percentages are relative to the total number of plants sampled: in 1987, 55 *G. crinita* and 60 *D. carota*; in 1988 and in 1989, 40 of each species. Differences were tested with chi-squared tests.

Year	<u><i>D. carota</i></u>		<u><i>G. crinita</i></u>		Difference	χ^2 p value
	Number	%	Number	%		
1987	6	10.0	13	23.6	ns	.05
1988	7	17.5	13	32.5	ns	.12
1989	<u>3</u>	<u>7.5</u>	<u>11</u>	<u>27.5</u>	Gc > Dc	.02
Total	16	11.4 %	37	27.4 %		

(b) Types of damage suffered by plants which did not produce seed heads, all plants from 1987 to 1989 pooled.

	<u><i>D. carota</i></u>		<u><i>G. crinita</i></u>	
	Number	%	Number	%
Whole plant eaten off	3	19 %	14	38 %
Plant shrivelled before seed heads ripe	5	31 %	9	24 %
All heads lost (shrivelled, eaten, or nipped off)	3	19 %	8	22 %
Unknown	<u>5</u>	<u>31 %</u>	<u>6</u>	<u>16 %</u>
Total	16	100 %	37	100 %

Effect of loss of stem-tops on *G. crinita*'s flower production

It was often not possible to ascertain why the stems of second-year *G. crinita* plants were damaged, but sometimes larvae of a species of Lepidoptera were found at the top of the plant where they appeared to be feeding on the young growing tip of the stem, young leaves, and occasionally flower buds. The larvae were particularly noticeable in August 1987, when 9 out of 32 plants that had lost their tops had larvae present on the stem, and in September 1988 and 1989 when larvae were present on, respectively, 5 out of 17 and 3 out of 10 stems without tops. Apparently identical larvae were seen on plants at Letchworth State Park. Two larvae were collected from there and successfully reared in 1989. The adults were identified as plume moths in the family Pterophoridae by Dr. John Franclemont (Cornell University). The genus was tentatively identified as *Stenoptilia* by Dr. Klaus Satler of the British Museum of Natural History, London, and Dr. Ferguson of the Systematic Entomology Laboratory, USDA (National Museum of Natural History, Washington, D.C.).

Dr. Ferguson, who now holds the specimens, believes the moth may be an undescribed species in the USA (pers. comm.). He intends to pursue the collection and identification of further specimens.

The loss of stem tops sometimes resulted in an increase in the number of flower heads produced. When numbers of heads present in August in 1987 and 1989 on plants that had lost their top were compared with those that had not, no differences were found (Mann-Whitney, $p > .05$). However, in both years plants which had lost their stem tops subsequently produced slightly more flowers in September than intact plants (1987: $n = 32$ plants with no top, 28 intact plants, $p = .0496$; 1989: $n = 8$ plants with no top, 32 intact plants, $p = .04$). Flower heads developed later in 1988 so numbers in September and subsequent numbers in October were analyzed. There was no difference in number of heads between the two groups of plants in September, nor in the number subsequently formed by October ($p > .05$, $n = 17$ plants with no top, 21 intact plants), although the trend was similar, i.e. the mean rank of numbers of heads formed on plants which had lost stem tops was greater than that of intact plants.

Seed dispersal

The period over which seed dispersal occurred extended from October to April or May the following year for both species, with most seed dispersing in the late fall or early winter (Fig. 4.2). It was assumed that all of the disappearance of seed from capsules or heads was due to dispersal. This might have been a slightly optimistic assumption for *G. crinita*. Capsules that were inspected when collected for seed counting or other experiments were sometimes found to be infested with larvae of another species of Lepidoptera. Two specimens of the larvae were collected and raised in 1989. The adults were identified as moths of the species *Endothenia habesana* by Dr. Franclemont. Independently, the same species was identified by Dr. Jerry Powell of the University of California at Berkeley from specimens collected by Daniel Rubinoff from *G. crinita* capsules on the Natural Area roadside (Robert Dirig, Cornell University; pers. comm.).

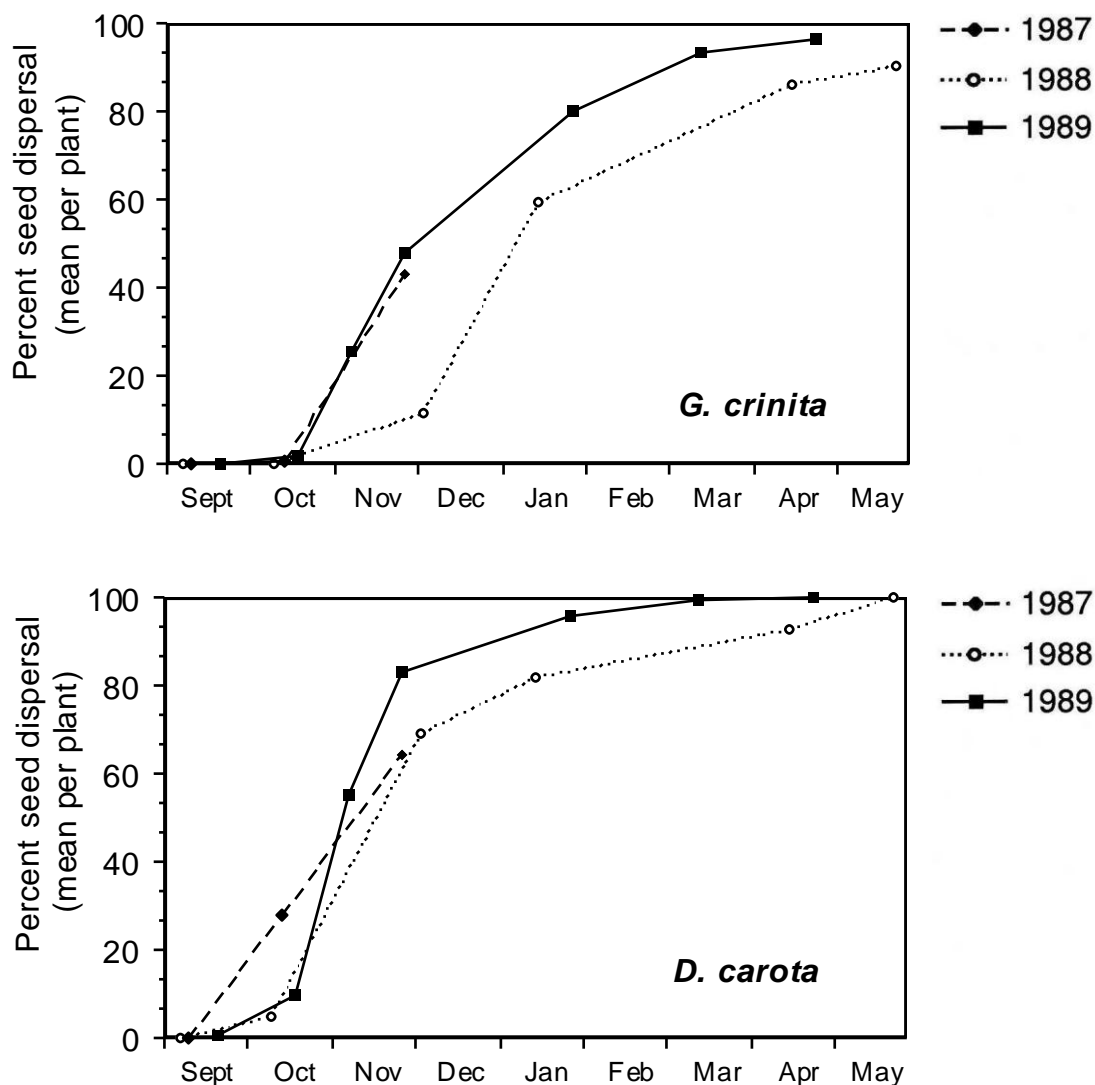


Fig. 4.2. Mean percent seed dispersal per plant, for *G. crinita* and *D. carota* at the Radio Lab over fall and winter. Values were calculated for each plant by averaging the percent of seed dispersed from each capsule ($n = 60$ *D. carota* plants and 55 *G. crinita* plants in 1987, 40 of each in 1988 and 1989).

Infestation rates varied from year to year at the study sites (Table 4.4a), and the disappearance of some seed could have been due to seed consumption by the larvae. However in 1988 and 1989 infestation rates were low (Table 4.4a), so the estimates of amount of seed dispersed at different dates were probably reasonably accurate for these years.

In addition to possible seed consumption, infestation of capsules sometimes resulted in a lower percentage of seed being dispersed, even if the larva that had been present in the capsule had died or had apparently left before eating much of the seed. This was because the presence of the larvae was almost always associated with the occurrence of persistent sticky threads (seen in collected seed capsules) which held the seeds in the capsule together and prevented dispersal. In 1988 and 1989, the numbers of capsules affected were similar to the infestation rates at the Radio Lab (Table 4.4b). This "stuck together" seed may never have been properly dispersed, but some seeds may perhaps have reached safe sites for germination once the parent plant rotted away.

Table 4.4. Effects of *Endothenia*: the proportion of *G. crinita* seed capsules infested, and the proportion of heads which dispersed <90% of their seeds.

(a) Infestation of *G. crinita* seed capsules with larvae of *Endothenia habesana*. The capsules were inspected either when collected for counting seeds per capsule or for other experiments.

<u>Site</u>	<u>Year</u>	<u>Number of capsules inspected</u>	<u>Number infested</u>	<u>%</u>
Radio Lab	1986	39	15	38.5 %
	1987	89	21	23.6 %
	1988	40	4	10.0 %
	1989	60	3	5.0 %
Letchworth	1988	30	8	26.7 %
	1989	20	0	0 %

(b) Total numbers of undamaged seed heads (capsules or umbels) of each species in November 1987-1989, and of these the number which had dispersed most of their seed by April the following year (data only for 1988 and 1989) at the Radio Lab field. Numbers of *G. crinita* capsules left in April that had seeds stuck together at the base of the capsule, presumably by the activities of *Endothenia* larvae, are also given for 1988 and 1989. These are all included in the number of capsules that dispersed <90% of their seed by April. (Numbers of plants in the samples were: 55 *G. crinita* and 60 *D. carota* in 1987, 40 of each species in 1988 and in 1989.)

<u>Year</u>	<u>Number of seed heads</u>				
	<u>Undamaged in November</u>	<u>>90% of seeds dispersed by April</u>	<u><90% dispersed</u>	<u>Lost</u>	<u>With seeds stuck together</u>
<i>D. carota</i>					
1987	64	[no data]			
1988	42	40	0	2	
1989	43	42	0	1	
<i>G. crinita</i>					
1987	245	[no data]			
1988	91	58	16	17	8 (11% of 91)
1989	138	106	10	22	9 (8% of 138)

The number of seed heads of *G. crinita* and *D. carota* that survived to successfully disperse their seed was compared in 1988 and 1989 by looking at how many seed heads per plant had dispersed over 90% of their seeds by April (Table 4.1). Although in October each year *G. crinita* had greater numbers of seed capsules, it suffered higher losses over winter. These losses in the 1988-89 winter resulted in no difference being detected between the two species in number of seed capsules or heads per plant that dispersed most of their seed by April 1989 (Table 4.1). In 1989-90, *G. crinita* just maintained its advantage despite losing more seed heads than *D. carota* (Table 4.1).

These comparisons slightly underestimate the seed output of *G. crinita*. Some *G. crinita* capsules had less than 90% of seed dispersed in April while all *D. carota* seed heads had dispersed more than 90% of their seed (Table 4.4b). Some of the *G. crinita* capsules with less than 90% of seed dispersed had seed stuck together by *Endothenia* larvae (Table 4.4b), but the others may have successfully dispersed some of their seed after April. At least some of this seed is still able to germinate in the same year (see Section III of Chapter 3). Average seed dispersal per plant increased after April in 1989 (Fig. 4.2), although by 23rd May 1989 only one out of the 16 remaining capsules that had less than 90% of seed dispersed in April had dispersed more than 90% of its seed by May 23rd. Also, *G. crinita* seed output may have been underestimated if any of the undamaged seed capsules that were present in late November or early December dispersed seed before being lost some time during the following weeks (Table 4.4b).

No data were collected for the winter 1987-88 but at a guess, with an estimated infestation rate by *Endothenia* larvae of 23.6% (Table 4.4a) and similar overwinter losses (say 17%), around 155 *G. crinita* capsules may have dispersed their seed, which is more than twice the number of undamaged *D. carota* seed heads (64), even if this species suffered no losses of those seed heads present in November (Table 4.4b).

Seed numbers and weights

At both the Radio Lab field and at Letchworth, *G. crinita* had higher total numbers of seeds per seed head and more filled seed per head than *D. carota*. However *D. carota* had heavier seed than *G. crinita* (Tables 4.1, 4.5). Only those capsules that were found not to contain any *Endothenia* larvae were used to obtain the figures for *G. crinita* because the larvae could have consumed some of the seeds in infested capsules. The proportion of filled seed per seed head was always greater for *G. crinita* than *D. carota* (Mann-Whitney tests, $p < .05$):

Median percentages:		1987	1988	1989
Radio Lab:	<i>G. crinita</i>	94.8	100.0	97.0
	<i>D. carota</i>	78.5	70.0	76.7
Letchworth:	<i>G. crinita</i>	-	100.0	97.4
	<i>D. carota</i>	-	81.2	82.6

Actual seed output of *G. crinita* would of course have been affected by the consumption of seed by *Endothenia* larvae. However, inspection of the median numbers of filled seed per capsule or umbel (Tables 4.1, 4.5) suggests that *G. crinita* can have at least 2 to 4 times as many seeds as *D. carota*. Infestation of capsules (and subsequent consumption of seed) by larvae would therefore have to be greater than that seen during this project (maximum 38.5%, Table 4.4a) to reduce *G. crinita*'s seed output per seed head to that of *D. carota*.

Table 4.5. Seed numbers and weights from *G. crinita* and *D. carota* plants at Letchworth State Park in 1988 and 1989. Differences were tested with Mann-Whitney U tests.

Year	<u>D. carota</u>			<u>G. crinita</u>			Difference	p value
	n	Median	(Range)	n	Median	(Range)		
<u>Total numbers of seeds per capsule or head</u>								
1988	27	110	(11-396)	15	362	(58-741)	Gc > Dc	.0003
1989	30	120	(16-376)	20	286	(67-487)	Gc > Dc	.0001
<u>Numbers of filled seeds per capsule or head</u>								
1988	27	90	(1-364)	15	361	(58-707)	Gc > Dc	.00004
1989	30	99	(0-364)	20	276.5	(65-470)	Gc > Dc	.00004
<u>Average seed weight (mg)</u>								
1989	19	0.407	(.261-.774)	20	0.052	(.042-.098)	Dc > Gc	.00001

It should be noted that the collection of ripe seed capsules relatively early in the reproductive season for both species, i.e. early to mid-October for *D. carota* and late October to mid-November for *G. crinita*, may overestimate the actual average numbers of seed per seed head for both species. Dale (1974) reported that the earliest-ripening seed heads of *D. carota* had the most seed. *G. crinita* may behave in the same way. The smallest plants seemed to flower last and had small seed capsules. Analysis of some data collected in 1989 confirmed this impression that small plants had small capsules and therefore less seed. The heights of the *G. crinita* plants from which seed was collected were measured to the nearest 0.1 cm and plotted against seed numbers per capsule (Fig. 4.3). Greater height was positively related to higher seed number per capsule.

While this relationship held for plants growing in the same year, it did not hold for comparisons between years. Height of the sample *G. crinita* plants, measured in October when upward growth had more or less ceased, was greatest in 1987 and lowest in 1988 (Kruskal-Wallis H = 15.70, multiple comparisons, $p < .05$; medians: 25 cm in 1987, 16 cm in 1988, 20 cm in 1989). However total number of seeds per capsule and numbers of filled seed per capsule showed the opposite pattern, being lowest in 1987 and highest in 1988 (Table 4.1, Kruskal-Wallis H = 26.98, $p < .05$). As more flowers were produced in 1987 (see above), the seed output between years appeared to be broadly comparable. *D. carota* did not vary significantly between years in height or seed number per umbel (Kruskal-Wallis tests, $p > .05$, median heights: 44 cm in 1987, 40 cm in 1988, 41 cm in 1989; median numbers of seed, see Table 4.1), although more umbels were produced in 1988 compared to the other two years (see above).

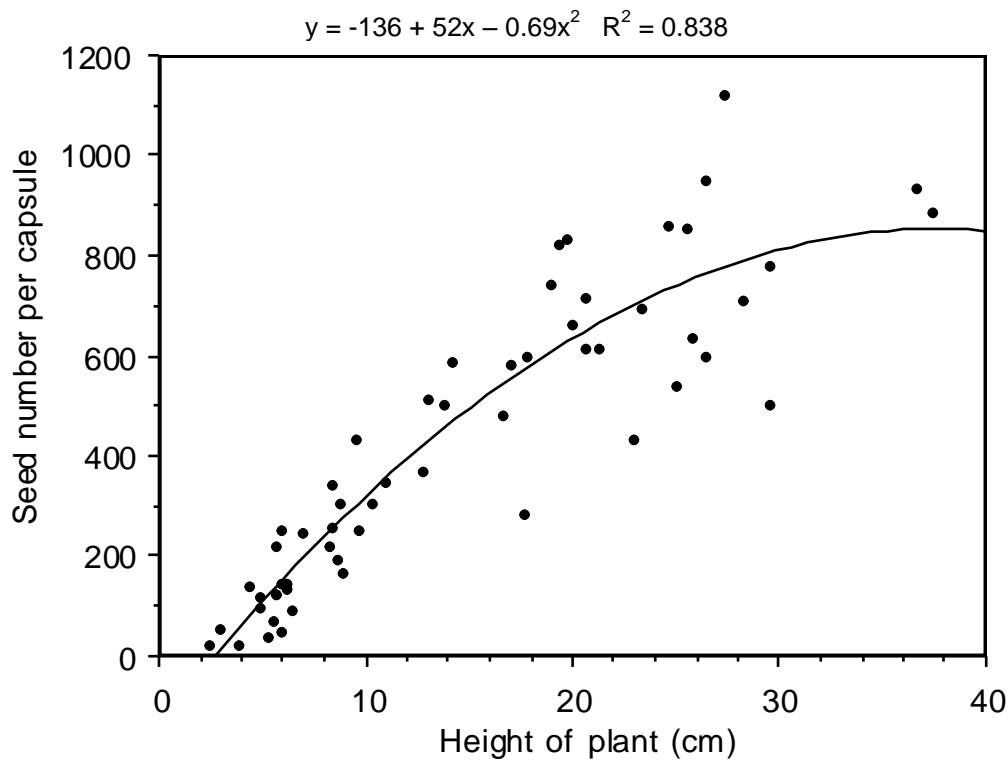


Fig. 4.3. Relationship between number of seeds per capsule, and plant height, for *G. crinita* at the Radio Lab in 1989 ($p < .0001$).

Timing of reproductive events

The data collected from the Radio Lab field, the Natural Area, and the Letchworth study site indicated that *D. carota* took longer to reach the reproductive stage than *G. crinita*. At Letchworth, of the survivors of 150 *D. carota* seedlings marked in the transects in 1987 only 2 flowered in 1988 and 5 more of the 26 survivors in 1989. Over the two years a total of 15 umbels were produced. In contrast, of the 163 *G. crinita* seedlings marked in 1987, all the 28 survivors flowered in 1988, and produced a total of 87 flower heads.

Similarly, at the Radio Lab none of the survivors of the *D. carota* seedlings marked during the microhabitat study in 1987 and 1988 had flowered by the end of 1989, whereas the stems of all of the surviving *G. crinita* plants elongated in their second year. In the clearings in the scrub in the Natural Area, where seeds of both species had been sown in fall 1987, all surviving *G. crinita* plants bolted in 1989 while only 8.2% of the *D. carota* plants present in the plots in July 1989 had elongated stems (73 out of 890 plants).

DISCUSSION

Seed numbers

The results reported for the three study sites in New York State provide no support for the hypothesis that the relative scarcity of *G. crinita* is due to its low reproductive output compared to the common biennial, *D. carota*. The combination of higher numbers of reproductive heads produced, more seeds per seed head, and greater frequency of reproductive events, meant that *G. crinita* had a greater seed output than *D. carota*.

In the context of average seed production by biennials (Hart 1977), both species have relatively low seed outputs. Yet *D. carota* is still very common. Hart used data in Salisbury (1942) for seed output of a range of British plants and found that the mean seed number per year for biennial plants was 28,780 while annuals produced on average 6,368 and perennials 5,869. Seed numbers per plant quoted in the literature on North American populations of *D. carota* are rather higher than those found in my project. Dale (1974) reported 1000-4000 seeds per plant, and Gross and Werner (1982) gave 1800 as the seed output. Neither study specified when and how the plants were sampled to arrive at these figures, but perhaps the sites had more fertile soils than my sites. For *D. carota* in chalk grassland in The Netherlands, During et al. (1985) reported that the average seed production was about 80 seeds per plant. In my project the most optimistic average figure calculated from median number of heads in September and total seed per seed head would give numbers of around 200-500 seeds per plant. Actual numbers dispersed would be closer to 80-100, calculated from median number of heads that had dispersed more than 90% of seed by April and numbers of filled seed per seed head.

For *G. crinita* the optimistic average would be around 1800-2700 seeds per plant and the actual number dispersed about 400-740 seeds per plant. These figures are of the same order of magnitude as those for several annual or biennial members of the Gentianaceae. Salisbury (1942) reported that *Gentianella amarella*, *G. germanica*, and *G. anglica* had seed numbers of 862, 623, and 295, respectively, although Kelly (1989a) gave figures an order of magnitude lower for *G. amarella* in chalk grassland in England (30-90). Batty et al. (1984) found seed output of the biennial *Gentiana nivalis* in montane grassland in Scotland ranged from about 100 to over 1000, but not tens of thousands. Spira and Pollack (1986) found that two biennial *Gentiana* species, *G. tenella* and *G. prostrata*, in alpine meadows in California had seed numbers ranging from 149–317 per plant.

The very high average seed numbers for biennials given by Hart (1977) were heavily influenced by the huge seed production of biennials that were found in intermittently open habitats, such as woodland clearings (average of 48,292 seeds per plant) or mud around fluctuating ponds (average of 45,450). It is worth noting the influence of phylogeny within habitats. The three out of 18 species in Salisbury's data for woodland clearings that had the highest seed numbers (over 85,000 per plant) were biennials in the family Scrophulariaceae.

Hart (1977) found that biennials in all of Salisbury's habitat categories, which ranged from open ground to closed vegetation, had greater seed output than annuals or perennials, except in semi-open habitats, i.e. herbaceous swards with small gaps. For this habitat her figures were 822 seeds per plant for biennials, 3649 for annuals, and 2612 for perennials. Hart made a connection with phylogeny, as she ascribed this low figure for biennials to the occurrence of several gentians in this habitat category and suggested that perhaps high survival as seedlings due to mycorrhizal associations might enable lower seed production to be a viable option. However Hart did not specify the source of her categorization of life history for Salisbury's species. A repeat calculation, using the standard reference work on the British flora (Clapham et al. 1987), gave different average values of seed output: biennials 2271 seeds per plant (6 species), annuals 2445 (4 species), and perennials 1715 (9 species). In this categorization I ignored species that have "transitional" life history descriptions in Clapham et al. (1987), for instance "annual to perennial" and "annual to biennial." If these are included in biennials, the average number of seeds per plant is only slightly different (3034; 9 species). Hart mentioned five biennial gentian species. Only four *Gentiana* species listed by Salisbury are biennials in Clapham et al. (1987) and these do have a relatively low average seed output (526). The other biennial member of the family Gentianaceae in semi-open habitats (*Centaureum erythraea*) had a much higher seed production (10,840).

Salisbury's (1942) semi-open habitat is probably the most similar of all his categories to those habitats which *G. crinita* and *D. carota* favor in New York State (Chapter 3, Sections I and II) and which also equate to Grubb's (1976) category of permanently open, i.e. unforested, swards where

small gaps always occur. Grubb suggested that plants in these "predictable" permanently open situations could be expected to have a lower seed output than species in unpredictable, intermittent habitats such as woodland clearings. He put *D. carota* and *Gentianella* species (seed numbers of 300-800 per plant) in the former category. My data on *D. carota* and *G. crinita* would seem to fit here as well, not only in terms of the species' requirement for permanently open conditions because they have short-lived seed banks, as discussed in the preceding chapter (Section III), but also in terms of seed production per plant.

Grubb (1976) questioned why some species in his permanently open habitat category produced so many more seeds than others, e.g. *Centaureum erythraea* with some 11,000 seeds per plant. He noted that the higher seed numbers in the family Gentianaceae were associated with the more widespread species. This connection between seed output and frequency of occurrence of a species was explored by Salisbury (1942). He returned to this theme again and again in his classic work "The Reproductive Capacity of Plants" and it appeared to be a concept of far greater interest to him than the relationship between life history and seed output. He proposed two alternative hypotheses, the first that greater reproductive output was related to greater frequency of occurrence, and the second that less common species which had greater specialization in habitat requirements would have greater seed production in order to reach the fewer suitable habitats that were available to them. Salisbury gave a number of examples from his data on the British flora that supported his first hypothesis. One example was the association of greater frequency of occurrence of the monocarpic *Gentianella* species (called *Gentiana* in 1942) with higher seed output per plant. He also included a perennial polycarpic species (*Gentiana pneumonanthe*) that had the greatest seed output but lower frequency of occurrence than the commonest monocarpic species. He suggested that this might be explained by his alternative hypothesis, i.e. *G. pneumonanthe* had more specialized habitat requirements.

Salisbury's examples were among closely related species or genera, but there seems no obvious reason why plants from different genera which have the same life history and an equal dependence on seed production as a means of reproduction should not also follow the pattern of greater seed output and greater frequency of occurrence, or alternatively greater habitat specialization and greater seed production. Comparison of seed output of *D. carota* and *G. crinita* does not support Salisbury's first hypothesis as the rare *G. crinita* had a greater seed output than the common *D. carota*. The higher output of *G. crinita* might be more related to its habitat requirements, as suggested by Salisbury's second hypothesis, and this issue of habitat specialization is explored in Chapter 5.

The greater reproductive output of *G. crinita* is perhaps another example of a general characteristic of rare plants that was first suggested by Rabinowitz (1981), i.e. that rare species have traits that allow them to persist despite their small population sizes. Rabinowitz and her colleagues found that rare prairie grasses had greater competitive ability than common species and less variable reproductive output (Rabinowitz 1981, Rabinowitz et al. 1984, Rabinowitz et al. 1989). The findings for relative reproductive output of *G. crinita* and *D. carota* over the years 1987-1989 hint that *G. crinita* may also have less variable output than the common *D. carota*. In the year when a higher number of *G. crinita* flowers was produced, significantly fewer seeds per capsule were recorded, while *D. carota* had more umbels in one year but relatively constant seed numbers per seed head. However there are not enough data to be at all certain about this pattern. Also the relative quality of the seeds in different years was not examined to see, for instance, if *G. crinita* seed produced in 1988 had lower viability than that produced in 1987.

Seed mass

D. carota has heavier seed than *G. crinita*, but the significance of this fact in terms of the habitats that *G. crinita* can occupy and thus its relative scarcity is not clear. As described in Chapter 3, neither species requires open bare ground to regenerate successfully. Although neither can survive and

reproduce in shady scrub habitats, both can survive in more or less closed herbaceous swards, which lack bare ground "gaps." This is in contrast to the biennial *Verbascum thapsus*, which has seeds of similar weight (0.064 mg) to *G. crinita*, yet requires such gaps to regenerate successfully (Gross & Werner 1982, Gross 1984). The results for *G. crinita* and *D. carota* in my study parallel Grubb's findings (1976) that short-lived species in the predictable habitat of almost continuous turf in chalk grassland had wide-ranging seed weights, from *Blackstonia perfoliata* (0.0107 mg; Gentianaceae) to *G. amarella* (0.087-0.17 mg), *G. anglica* (0.128 mg, Salisbury's 1942 data), *G. germanica* (0.15 mg, Salisbury's data), and *D. carota* (1.5 mg) and *Seseli libanotis* (1.69 mg). The weights of *G. crinita* and *D. carota* found in my work were within this range (Tables 4.1, 4.5).

Causes of losses to reproductive output and implications for conservation management

G. crinita suffered greater losses of reproductive plants and seeds, particularly to herbivory, but not enough to reduce the seed output to that of *D. carota*. It may be that *D. carota*, an introduced species in North America, lacks some of the herbivores that attack it in its native Eurasian locations, although no comparisons appear to have been made. Most of the losses to *D. carota* were caused by heads shrivelling. Dale (1974) noted that in Canada senescence frequently occurred while plants still had immature umbels, so perhaps in northern latitudes development of further umbels ceases once seed is set in one or more umbels that have flowered earlier in the season.

Seed predators can have significant effects on rare plants (Harvey 1985, Menges 1988) and on more widely distributed plants (Greig-Smith & Sagar 1981, Louda 1982, 1983). Other members of the Gentianaceae are attacked by seed-eating larvae, for instance Kelly (1989a) found that a high proportion *Gentianella amarella* fruits were attacked by a gall midge larva (*Cecidomyiidea*, possibly *Dasineura*) in some years. The amount of damage to *G. crinita* also varied from year to year and may sometimes be greater than that observed during my project. However because it is short-lived it might never suffer as much damage, for example, as that inflicted on a perennial gentian, *Gentiana saponaria*, by *Endothenia habesana* in Ohio. Ninety percent of the capsules on plants of *G. saponaria*, which is an endangered species in Ohio, were infested by larvae and classed as "non-functional" over a four-year study (Windus 1990). Spira and Pollack (1986) found that two biennial *Gentiana* species were much less damaged by mammal and insect herbivores than a perennial *Gentiana* species growing in the same habitat. It may be that polycarpic perennials have greater stability of population density in space and time compared to short-lived monocarpic species, and this may affect the relative amounts of damage that they suffer. Chew and Courtney (1991) found that plants with more stable population densities accumulated more damage from invertebrates and had higher infestation rates by Lepidoptera larvae than plants showing larger year-to-year density changes, though they did not specify which life histories were represented.

Simmonds (1946) found another *Endothenia* species in *Gentiana pneumonanthe* capsules in England and reported that it occurred on other gentian species, *Dipsacus* species, and *Plantago media* in Europe. In North America, *Endothenia habesana* also appears to be a generalist seed predator (Dr. John Franclemont, pers. comm.; and J. F. Gates, quoted in Windus 1990). While the presence of a generalist seed predator on a rare plant is not surprising, the association of larvae of a perhaps uncommon, specialist Pterophoridae species with *G. crinita* is unexpected. This result contrasts with work by Chew and Courtney (1991), who found that species of Lepidoptera larvae which had narrow diet breadth were associated with predictable and abundant host plants.

Damage to the flowering stem of *G. crinita* by larvae and/or mammals was associated in some years with slightly greater subsequent production of flowers compared to undamaged plants, or at least with no reduction in flower numbers. The tendency of *G. crinita* to "bush out" after mowing damage was noted by Thoreau (1906), Norton (1923) and during this study. Such recovery from damage has also been seen in some other plant species (Hendrix 1979, Paige & Whitham 1987) but not in other cases (Louda 1984, Menges 1988). In a study of the response of the biennial scarlet gilia, *Ipomopsis*

aggregata, to ungulate grazing, Paige and Whitham (1987) found similar overcompensation in flower production to that seen in *G. crinita*. However, as Crawley (1988) pointed out, it is difficult to understand why ungrazed plants would not therefore benefit from additional branching from lower down the stem. It may be that the quality of the seed produced from the "extra" flowers is lower. For example Crawley and Nachapong (1985) found that seeds from regrowth shoots of ragwort (*Senecio jacobea*) after defoliation by cinnabar moth caterpillars were much lighter than seeds from primary flowers. Seedlings that germinated from the lighter seeds had very poor survival in the face of interspecific competition compared to seedlings from heavier seeds developed on primary flowers. Paige and Whitham (1987) could find no evidence of lower seed quality, but Maschinski and Whitham (1989) suggested that the amount of compensation can vary depending on conditions such as nutrient supply, and that overcompensation in scarlet gilia occurred in favorable nutrient and moisture conditions. This might also be the case for *G. crinita*, as there was stronger evidence of overcompensation in the wetter years (1987 and 1989) than in the drought year of 1988.

Maschinski and Whitham also pointed out that the timing of damage was important. Grazing of scarlet gilia early in the growing season could allow compensation while late grazing might not. Mowing can damage second-year *G. crinita* plants and timing of mowing is an important factor for conservation managers to consider if they are using mowing as a tool to prevent scrub encroachment in *G. crinita* localities. *G. crinita* can produce new flowers even if mown as late as August (Norton 1923, and this study). However, while *G. crinita* can withstand mowing and can compensate for loss of flowers and buds, late mowing would seem likely to cause unnecessary damage to plants with developing fruits and seeds, and might affect the seed quality of new flowers in some way. Earlier mowing dates would be preferable, timed to occur before most buds develop, i.e. in May, June, or into early July in New York State, depending on the seasonal conditions for growth. Unless there is rapid regrowth or invasion by woody species, it would be preferable to mow infrequently, at least every other year, to allow *G. crinita* to flower undisturbed in some years. If biennial peaks in flowering occur in a population, mowing should be done in intervening years when most of the population is in the rosette stage.

G. crinita seems able to tolerate grazing by domestic stock if this is not too heavy (Mark Loeshke, Iowa Heritage Program; Paul Wiegman, Western Pennsylvania Heritage Program) and so stock grazing could be used as a management tool to control scrub invasion. *G. crinita* populations were found in two cattle-grazed pastures in New York State, and at one of these had persisted at least for the last 10 years (Robert Dirig, pers. comm.).

The potentially deleterious impact of deer grazing on flowering *G. crinita* populations, especially late in the season when recovery would be difficult, may need to be evaluated by conservation managers. At the Radio Lab field deer grazing did not appear to be a major problem even though deer numbers in the area were regarded as high (buck take of around 3 per square mile; information from W. Dukelow and R. Gotie, State Department of Environmental Conservation, Cortland Office). However, deer were observed to cause greater damage locally, for example in secluded clearings in scrub thickets in the Natural Area or east of the Radio Lab, where deer could browse relatively undisturbed. All of the flowers and seed capsules could be removed from the plants in these situations. *G. crinita* populations may therefore benefit from increased scrub clearance, not only to reduce shading but also to discourage deer grazing by reducing available cover.

CHAPTER 5

THE SPATIAL DISTRIBUTION AND RELATIVE RARITY OF *Gentianopsis crinita* IN THE LANDSCAPE

INTRODUCTION

Theoretical papers and empirical studies of common biennials have emphasized the importance of high survival rates of plants in the vegetative stage as well as, or instead of, high reproductive output (Hart 1977, Silvertown 1983, Klinkhamer & de Jong 1983, Klemow & Raynal 1985, de Jong & Klinkhamer 1988). The results already described in Chapters 3 and 4 indicated that the rare biennial, *Gentianopsis crinita*, can have a higher reproductive output than the common biennial, *Daucus carota*, when the two species are growing together in the same habitats. My study has also shown that *G. crinita* can survive and reproduce across as wide a range of successional habitats as *D. carota* and that it does not seem to be particularly restricted by lack of suitable microhabitats for regeneration or by poor seed dispersal capability (Chapter 3). Given these findings the question remains as to why *G. crinita* is in reality much more scarce than *D. carota* in the North American landscape. What factors are influencing its relative rarity through critically reducing the survival, growth and potential reproductive output of plants which are in the vegetative stage?

The results described in Chapter 3 indicate that both *G. crinita* and *D. carota* are restricted to open situations because of competition from large woody plants. However, an examination of published information on habitats favored by *G. crinita* (see Chapter 2) and the results of some preliminary attempts to grow the two species in various soil conditions in the greenhouse at Cornell suggested that *G. crinita* may not be able to tolerate such a wide range of soil conditions as *D. carota*. In particular the literature frequently refers to the association of *G. crinita* with moist, calcareous soils. I therefore decided to assess whether soil conditions were a major influence on *G. crinita*'s spatial distribution and relative rarity. This chapter will examine the following hypothesis: in unwooded landscapes the survival, growth and potential reproductive output of *G. crinita* plants in the vegetative stage are limited by a narrow range of soil conditions, i.e. the species has a restricted edaphic tolerance.

The influence of soil factors may interact in subtle and complex ways with competition from herbaceous plants and herbivory. Full analysis of these relationships was beyond the scope of this study but some observations on the role of herbivory and competition were made in addition to the investigation of soil factors.

As well as helping to explain the relative rarity of *G. crinita*, the experiments and observations described in this chapter were aimed at providing information that could be readily used by conservation managers who wish to locate populations, identify potential sites for introduction or re-introduction, and select preserves within which populations of *G. crinita* can survive over a relatively long time scale.

Three lines of investigation were followed and are set out in three sections in this chapter. Section I: A general survey of *G. crinita* localities in New York State to indicate the environmental features and habitat characteristics associated with the occurrence, relative abundance, and reproductive performance of the species across a range of sites in the landscape. Section II: At a more local scale, within a site, observations on the distribution, survival and performance of marked plants of *G. crinita* and *D. carota*, including transplanted individuals, and association with measures of soil conditions, plant cover and incidence of herbivory. Section III: Greenhouse experiments to test the response of *G. crinita* and *D. carota* to a range of soil types and moisture conditions.

SECTION I. SITE SURVEY

To investigate the environmental features and habitat characteristics associated with localities that have populations of *Gentianopsis crinita*, a survey of a range of sites in New York State was undertaken during September and October 1989 (24th September to 18th October). A limited amount of information collected at other times during the project was also included in the results.

Materials and methods

Sites were identified from information supplied by local naturalists and State Heritage Program staff, and from field searches. A total of 32 localities were visited, and of these, 31 had extant populations of flowering *G. crinita*, while *G. crinita* was present in 1988 and in previous years at the remaining site. The distribution of the sites in New York State is shown in Figure 5.1. Each site was subjectively defined as an area with a more or less continuous population of *G. crinita*. Where habitat conditions appeared to change spatially and the distribution of the plants was markedly discontinuous, the locations of these separate populations were treated as separate sites.

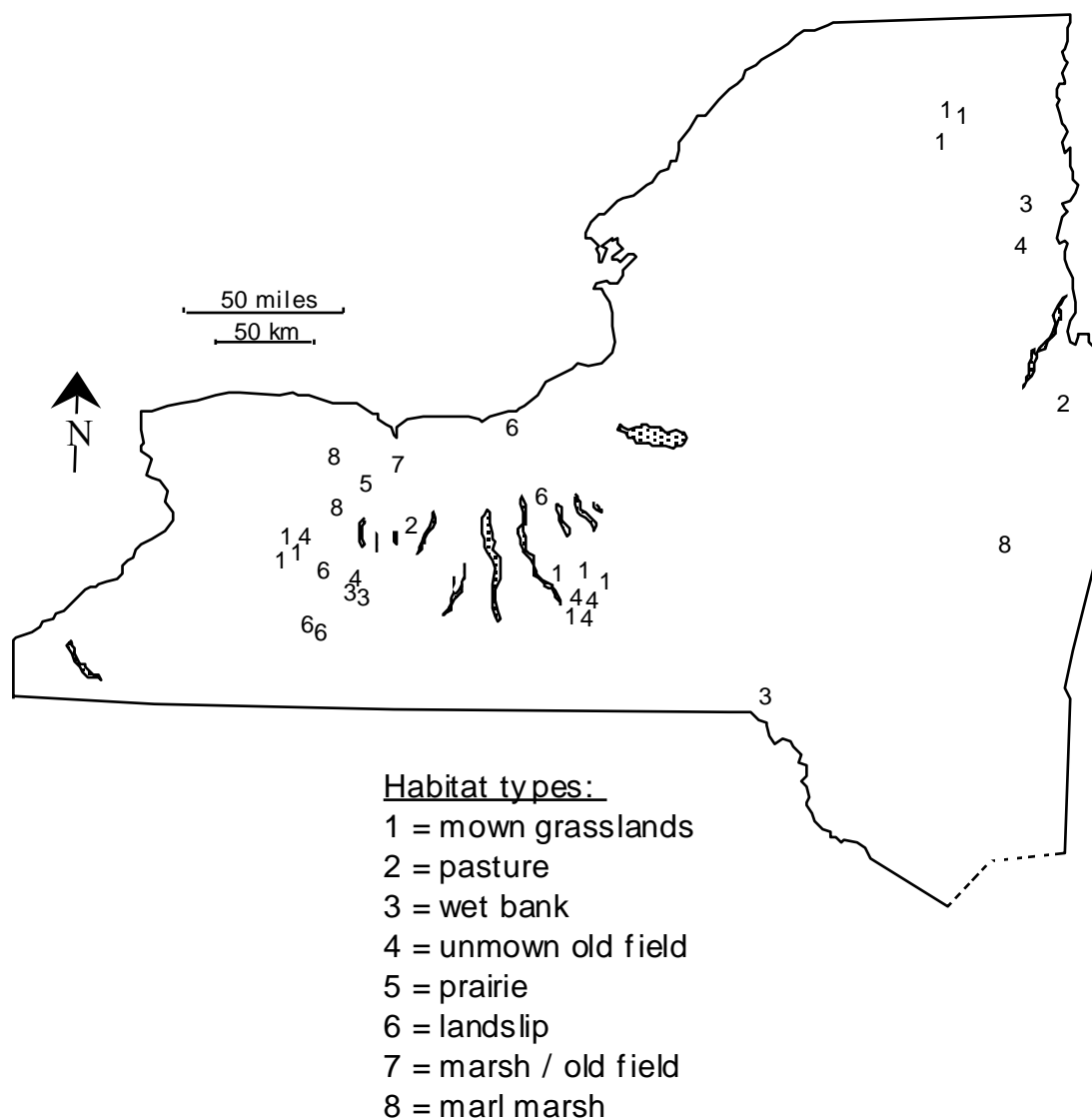


Fig. 5.1. Location and habitat type of sites surveyed in New York State during September and October 1989. The eight habitat types are described in the results section.

Seven of the sites originated from the deliberate introduction of seed, but populations have subsequently persisted at these sites for considerable periods. Three populations have been present for at least 20 years, three for 35 years and one for 10-15 years, when *G. crinita* was re-introduced after initial introduction 35 years ago (G. Chase, R. Pappert; pers. comms.).

The survey was carried out in the fall primarily because only at this time are populations of *G. crinita* easily visible, although most sites had been visited at least once before September 1989. In addition, one aim of the survey was to assess relative reproductive performance by recording information on flowering.

The following information was collected for each site:

1. Habitat type and management. A subjective categorization was made of readily recognizable habitat types present at each site, e.g. roadside, landslip or pasture. Any signs of management and potential conservation problems were also noted.
2. List of other species. Species identifications were made or checked by F. R. Wesley (Cornell). Nomenclature follows Mitchell (1986).
3. Elevation, recorded from U.S.G.S. topographical maps.
4. Slope angle in degrees across the site, measured with a clinometer.
5. Aspect, i.e. one of the 8 compass points.
6. Percent cover of bare ground, rock, moss, short herbaceous vegetation (< 25 cm), tall herbaceous vegetation (≥ 25 cm), short woody plants (< 1 m tall) and tall shrubs and trees (≥ 1 m tall). These categories are referred to by the general term "plant cover" in the results. Cover was estimated from a maximum of 10 randomly located 1 m by 1 m plots. Plots had to include *G. crinita* except for sites with one plant or none flowering in 1989. In these sites plots were located within the area occupied by the population in previous years.
7. Soil samples from the rooting zone. Observations on root depth of *G. crinita* at the Radio Lab site indicated that roots of flowering plants could extend to about 10 cm depth, although first-year plants had roots often less than 5 cm deep in the soil by mid-September 1989. At several sites soil depths were sometimes less than 10 cm over hardpan or rock, therefore at each site a volume of soil was collected (with a soil corer) equivalent to 15 ten cm depth cores, 2 cm in diameter. Samples were taken not more than 10 cm away from flowering *G. crinita*.

From the well-mixed composite sample for each site, a subsample was analyzed by the Cornell Nutrient Analysis Laboratories for pH, loss on ignition (an index of organic matter), extractable phosphorus, potassium, magnesium, calcium, iron, aluminum, manganese, and zinc. Soil pH was determined from a 1:1 (by volume) soil: water suspension. Loss on ignition was determined by drying the soil at 50° C for one hour, then igniting it at about 500° C for two hours. Nutrients were extracted with 10% sodium acetate in 3% acetic acid buffered to pH 4.8, using a 1:5 (by volume) soil: solution ratio. Potassium, magnesium, calcium, manganese, iron, aluminum and zinc were determined by atomic absorption. Phosphorus was determined colorimetrically by stannous chloride reduction. I analyzed the particle size distribution from another subsample by the hydrometer method (Allen et al. 1974) with the assistance of Ms. E. Lucas from Cornell's Agronomy Department. However soils which had high calcium levels were not treated with acid to break down calcium concretions, contrary to the method suggested by Allen et al. (1974), because field texture conditions where these concretions occurred were considered to be more akin to the texture measurements made on untreated samples.

While the samples were being collected, observations were made on signs of waterlogging in the upper layers of the soil profile. The presence of orange mottles, blue/grey gleyed soil, or surface peat accumulation were noted and the depth at which these signs occurred.

8. Number of flowering *G. crinita* plants.
9. Extent of the population, measured by pacing out the area and converting the result to meters.
10. Total number of "flowers" per *G. crinita* plant, and height of plants to the base of the uppermost flower (to the nearest 0.5 cm), recorded from a random sample of 50 plants or from all plants if the

population size was less than 50. "Flowers" included any reproductive head from bud to seed capsule stage, either damaged or undamaged, or flower stems where heads had been nipped off (as described in Chapter 4). The aim was to obtain an estimate of the maximum potential reproductive output from the sites rather than a count of actual numbers of undamaged heads at a particular survey date. This was because sites probably suffered variable levels of herbivory, in particular plants at sites surveyed later could have suffered more damage (see Chapter 4).

Data analysis

Data were summarized in terms of overall ranges and averages and also within the habitat types so that conservation managers interested in surveying for potential sites, habitat management, introduction or re-introduction can more readily assess which sites in their area might be suitable for *G. crinita*. Possible relationships between site factors such as soil chemistry and *G. crinita*'s density and reproductive performance were investigated using non-parametric statistics as the data were generally not normally distributed.

The simple count of flowering plant numbers was not used to look at relationships between site factors and abundance of plants as population sizes may simply reflect the area of available habitat. Density, i.e. number divided by population extent, was therefore used to represent relative abundance with regard to how favorable particular sites might be for survival. This measure assumes that the sites were relatively homogeneous with respect to conditions suitable for *G. crinita*. Relative reproductive performance among sites was represented by median numbers of flowers per plant of the plants sampled at each site. Height was also used to give an indication of relative reproductive performance. Both measures were analyzed in relation to soil factors and categories of amount and type of plant cover, i.e. bare ground, moss cover, short herbaceous vegetation, etc.

Soil moisture indices

The particle size distribution data and the information on presence of waterlogging in soils were used to construct two indices of soil moisture because direct measurements would have been affected by "chance" daily rainfall during the survey period.

A "waterlogging index" was devised by assigning soils to one of three classes: 1) signs of waterlogging in the upper 5 cm of soil, 2) waterlogging below 5 cm, 3) no signs of waterlogging. The index should reflect moisture conditions over a period of time (at least one or two seasons) as these signs are used in long term soil classification schemes (e.g. Soil Survey of Tompkins County, USDA 1965).

The particle size analysis was used to assign soils to 6 "available water" classes as defined by Etherington (1982). At soil moisture tensions between field capacity and permanent wilting point, relatively higher quantities of the water available to plants are associated with soils composed of particles of moderate size, i.e. silts, or soils which have roughly equal proportions of particle sizes, e.g. clay loams or loams (Lund 1959, Salter & Williams 1967). At the two extremes of particle size distribution relatively less water is available to plants. In sandy soils the large gaps between the sand particles are mainly filled with air while in clay soils the clay particles are so small that much of the water is held at tensions beyond the permanent wilting point of many plants (Etherington 1982). In the range between field capacity and permanent wilting point the cm water available per cm depth of soil in Etherington's 6 classes are: 1 (the "driest") = 0.00-0.05 cm, 2 = 0.05-0.10 cm, 3 = 0.10-0.15 cm, 4 = 0.15-0.20 cm, 5 = 0.20-0.25 cm, 6 (the "wettest") = 0.25-0.30 cm. This index gives an almost "absolute" measure of water availability that is independent of year to year fluctuations in water supply. It is only a potential indication of moisture however, unlike the waterlogging index. Local conditions, for instance presence of a spring or stream, might override the influence of particle size on available moisture levels.

Results

Habitat Types and Associated Species

Many of the populations occurred in habitats that were being managed or had been managed in the past, rather than in truly natural, pristine habitats. Although species lists were not exhaustive, some 260 other species were recorded during the survey (Appendix II), including representatives from quite a wide range of habitats. In particular the lists included species commonly found in habitats with a history of management, such as herbaceous perennials typical of old fields. These were recorded at most sites (Appendix II), for example *Fragaria virginiana*, *Aster novae-angliae*, and *Euthamia graminifolia* occurred in over 75% of the sites. *Daucus carota* was also one of the most frequently recorded species. Woody colonizers of old fields were frequent, particularly *Cornus foemina* subsp. *racemosa*. Species lists often included wetland species, especially those found in fens. Other members of the Gentianaceae were present occasionally, as well as rare or uncommon species from other families.

Some examples of species typical of each habitat are given below under each habitat category. The number of examples of each category that were visited during the survey is given in parentheses. It should be noted that although almost all known sites in New York State were surveyed, the distribution of sites between habitat categories was probably biased towards accessible sites such as roadsides where populations of *G. crinita* were easy to spot. The frequency of different species recorded during the survey probably also reflected this bias.

1. Mown Grasslands (10)

Either old fields or roadsides, mown for recreational and aesthetic purposes or for road maintenance and safety. These grasslands were not necessarily cut every year, for instance the roadside adjacent to Cornell's Fringed Gentian Natural Area was last mown in 1986, before being mown again in 1990. As well as the old field species mentioned above, typical species included other native *Aster* and *Solidago* species (e.g. *Aster lateriflorus*, *A. pilosus* var. *pringlei*, *S. canadensis*, and *S. nemoralis*) and introduced species (e.g. *Prunella vulgaris*, *Leucanthemum vulgare*, and *Plantago lanceolata*).

2. Pastures (2)

The two sites were grazed by cattle but apparently not intensively. Not much trampling was evident, and woody shrubs and trees were present in both sites, for instance *Malus pumila*, *Juniperus communis* (abundant in one site) and *Cornus foemina* subsp. *racemosa*. *Potentilla fruticosa*, an uncommon shrub species generally restricted to fens in New York (F.R. Wesley, pers. comm.) was also present in one site.

3. Wet banks (4)

These were sloping banks above or below roadsides, often with rock outcrops, small springs, or seeps. These sites may have been infrequently cleared of woody vegetation, for instance one site was underneath a power line. *Carex* and *Juncus* species were typical, e.g. *Carex hystericina*, *C. tribuloides*, *C. vulpinoidea*, *Juncus effusus*, and *J. tenuis*. The rare sedge *Carex complanata* was also recorded at one site. Dicotyledonous species included two *Spiranthes* species and two gentians (*Gentianella quinquefolia* and *Gentiana clausa*). Peaty soils were characteristic, and a typical species of these soils, *Drosera rotundifolia*, was recorded at two sites.

4. *Unmown old fields* (6)

These were fields reverting from past agricultural use, but did not appear to be managed at all, in contrast to category 1. However, their flora was similar to sites in this category.

5. *Prairie* (1)

Remnant prairie sites are also known as "oak openings" in New York State (Shanks 1966). The *G. crinita* locality was dominated by species typical of tall grass prairies of the mid-west (Shanks 1966), principally *Sorghastrum nutans*, *Andropogon gerardii*, and *Schizachyrium scoparium*. Other characteristic species included *Asclepias tuberosa* and *Monarda fistulosa*.

6. *Landslips* (5)

These were on unstable sloping ground, usually below earthy cliffs in glacial deposits, and were dissected with gullies. The sites had been colonized by the same species, both native and introduced, that were also present in most of the habitats resulting from human disturbance and management, i.e. the old fields and roadsides. For example *Aster lateriflorus*, *Solidago canadensis*, and *Euthamia graminifolia* were recorded at both kinds of site. Other less common species found on the landslips included *Shepherdia canadensis* and *Lonicera dioica*, and in wet areas *Parnassia glauca* and *Equisetum variegatum*.

7. *Marsh/old field* (1)

This site was transitional between a lakeshore fen and trailside grassland at the edge of scrub. Plants typical of fens or rich fens (F.R. Wesley, pers. comm.) were present, such as *Potentilla fruticosa*, *Equisetum variegatum*, and the rare *Pedicularis lanceolata*. *Gentiana andrewsii* was also recorded.

8. *Marl marshes* (3)

These were low lying localities, on marly soils and close to lakes or streams. They all appeared to have been associated with past mineral extraction, either for marl or sand and gravel, and two were bordered by *Typha* swamp. Wetland species such as *Scirpus atrovirens*, *Eupatorium rugosum*, *Juncus torreyi* and *Helianthus giganteus* were present, and one site had two of the fen species seen at the marsh/old field site, i.e. *Potentilla fruticosa* and *Pedicularis lanceolata*.

Elevation, slope and aspect

Most sites were flat or gently sloping (Table 5.1); only the landslips and wet banks had steep slopes. Populations of *G. crinita* were found at a range of elevations (73 - 576 m). Aspect also varied (Table 5.2). A comparison of populations on north and east slopes (n = 12) with ones on south and west slopes (n = 12), revealed that the north and east localities were generally lower than the south and west localities, even given the small sample sizes (p = .049, Mann-Whitney test).

Table 5.1. Summary of topographic, soil and population data collected from 32 *G. crinita* sites in September and October 1989.

	Minimum	Median	Maximum
Elevation (m)	73	336	576
Slope (°)	0	3	25
<u>Soil:</u>			
pH	5.9	7.6	8.2
Loss on ignition (%) (organic matter)	2.2	6.8	34.8
P (ppm)	0*	0.8	13
K (ppm)	23	43	176
Mg (ppm)	22	247	765
Ca (1000 ppm)	0.28	2.72	63.88
Fe (ppm)	0*	4	41
Al (ppm)	5	16	77
Mn (ppm)	6	27	106
Zn (ppm)	0.1	0.7	8
Clay (%)	2.0	18.7	50.8
Silt (%)	1.0	38.2	56.3
Sand (%)	4.0	39.9	97.0
<u>Flowering <i>G. crinita</i> plants:</u>			
Population size (#)	0	90	12,300
Population extent (m ²)**	12	472	30,000
Density (#/m ²)**	0.001	0.207	3.255
Median height (cm)	9.5	18.3	34.5
Median # flowers per plant	1	2	8

* not detectable

** n = 29 sites; at 3 sites in 1989 only 1 or 0 plants flowered

Table 5.2. Aspects of 29* *G. crinita* sites surveyed during September and October 1989. The sites in groups A and B were used in the comparison of elevation with aspect (A lower than B, $p = .049$, Mann-Whitney test).

	Aspect	Number of sites
Group A: {	North	2
	Northeast	8
	East	2
	Southeast	4
Group B: {	South	3
	Southwest	9
	West	0
	Northwest	1

* Three of the 32 sites were flat.

Cover types

As the description of habitat types indicated, populations were found in open conditions, though plants were seen close to edges of scrub or within the borders of open woodland. Percent cover of trees and shrubs was generally low (Fig. 5.2). However, bare ground was not extensive either. By definition, landslips had relatively high percents of bare ground (Fig. 5.2) but often also had a mosaic of other cover types including scrub and clumps of trees, as described for the Letchworth site (Chapter 2). Most of the sites were dominated by short herbaceous plants less than 25 cm in height, although the relative cover of tall and short herbs no doubt reflected management history. For instance, tall herbs were important in unmown old fields and the prairie (Fig. 5.2). *G. crinita* populations did not seem to be particularly associated with sites with high moss cover; percents varied but were almost all < 20% (Fig. 5.2).

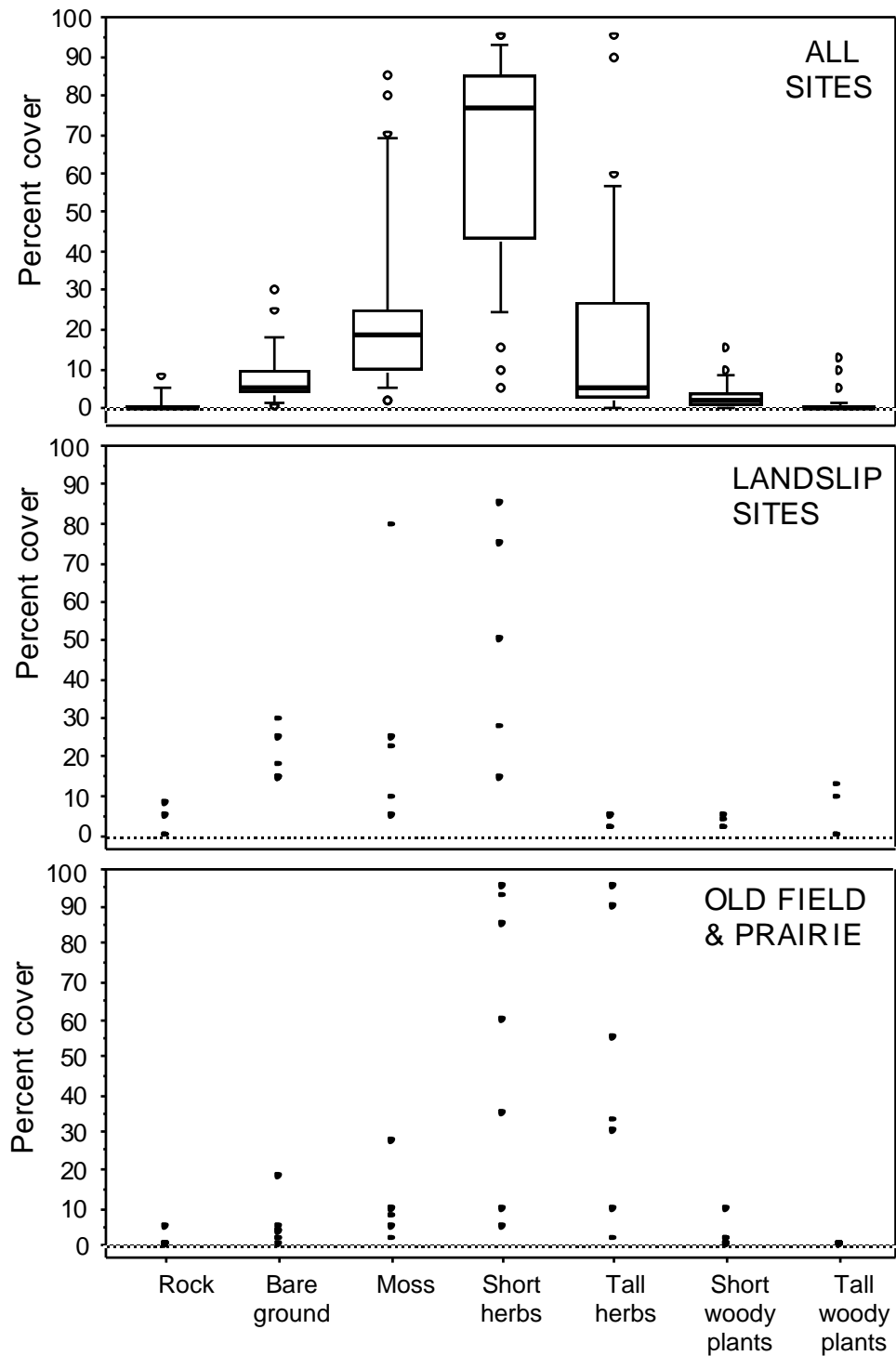


Fig. 5.2. Ground cover at the 32 *G. crinita* sites (median = horizontal line, quartiles = box, 10th-90th percentiles = vertical line, <10th, >90th = dots), at 5 landslip sites, and at 7 old field and prairie/oak opening sites, measured in 1 x 1 m plots in 5% cover classes (trace amounts assigned a value of 2%). Short herbs were < 25 cm tall, short woody plants were < 1 m tall.

Soil types

Soil chemistry and organic matter

G. crinita was not restricted to calcareous soils (the pH range was 5.9 to 8.2), but 75% of the sites had a pH above 7, and 44% were over 7.6. Around this pH free calcium carbonate may be present (USDA 1965). It should be noted however that pH is variable depending on moisture conditions. Long term waterlogging can reduce the pH in alkaline soils (Etherington 1982) so that plants in the field may not always experience the high pH values recorded in the soil analyses, which were carried out on dried soil. When the pH of soils in different soil moisture classes were compared, for both the waterlogging index and available water index, the "dry" pH values were higher in the wetter sites ($.025 < p < .05$, Kruskal-Wallis test). This result suggests that wetter sites may actually have rather lower pH levels than the "dry" pH values would suggest and therefore have values more similar to those recorded from drier sites.

Levels of calcium in the soils varied widely (Table 5.1) and *G. crinita* was apparently able to tolerate levels over 60,000 ppm in the marl sites. High levels of calcium were not always related to high pH, for instance the prairie site had a pH of 8.0 but calcium was relatively low (2661 ppm). Another base, such as magnesium, may have influenced the pH here. The magnesium level recorded was 671 ppm, which is "very high" in agricultural fertility terms (Cornell Cooperative Extension 1990).

Among habitat types, landslips tended to have high pH and calcium levels (Fig. 5.3) probably because calcareous subsoil or parent material was either exposed or close to the surface, and of course marl sites had high pH and calcium levels. Grassland sites that had had some soil disturbance in the past (e.g. the bulldozing at the Radio Lab mentioned in Chapter 2) also had high pH and calcium levels (Fig. 5.3). The other three sites where the soil had been heavily disturbed (Fig. 5.3) either had evidence of bare ground and disturbance on aerial photographs from the 1960's or were reported to have been disturbed (D. Bassett, pers. comm.). At another site, the roadside adjacent to the Fringed Gentian Natural Area near Ithaca, there had been some soil disturbance in the past although pH and calcium levels were not among the highest. However, levels were higher than in undisturbed soil in the adjoining Natural Area (Chapter 2).

Other soil factors did not show such clear patterns among habitat types. Ranges and medians across all sites for these factors are given in Table 5.1. The organic matter index (loss on ignition) tended to be quite low in landslip sites (< 6%) while peaty soils on wet banks, as might be expected, had high levels (e.g. 34.8% at one site).

In terms of "fertility" from an agricultural point of view, most of the sites had infertile soils in relation to phosphorus and potassium levels, while magnesium levels were generally high (Cornell Cooperative Extension 1990). According to the Cornell Cooperative Extension classification, phosphorus and potassium quantities were "very low" or "low," i.e. 28 out of 32 sites had less than 4 ppm phosphorus and 24 sites had less than 65 ppm of potassium. In contrast 27 sites had "high" or "very high" levels of magnesium (greater than 100 ppm).

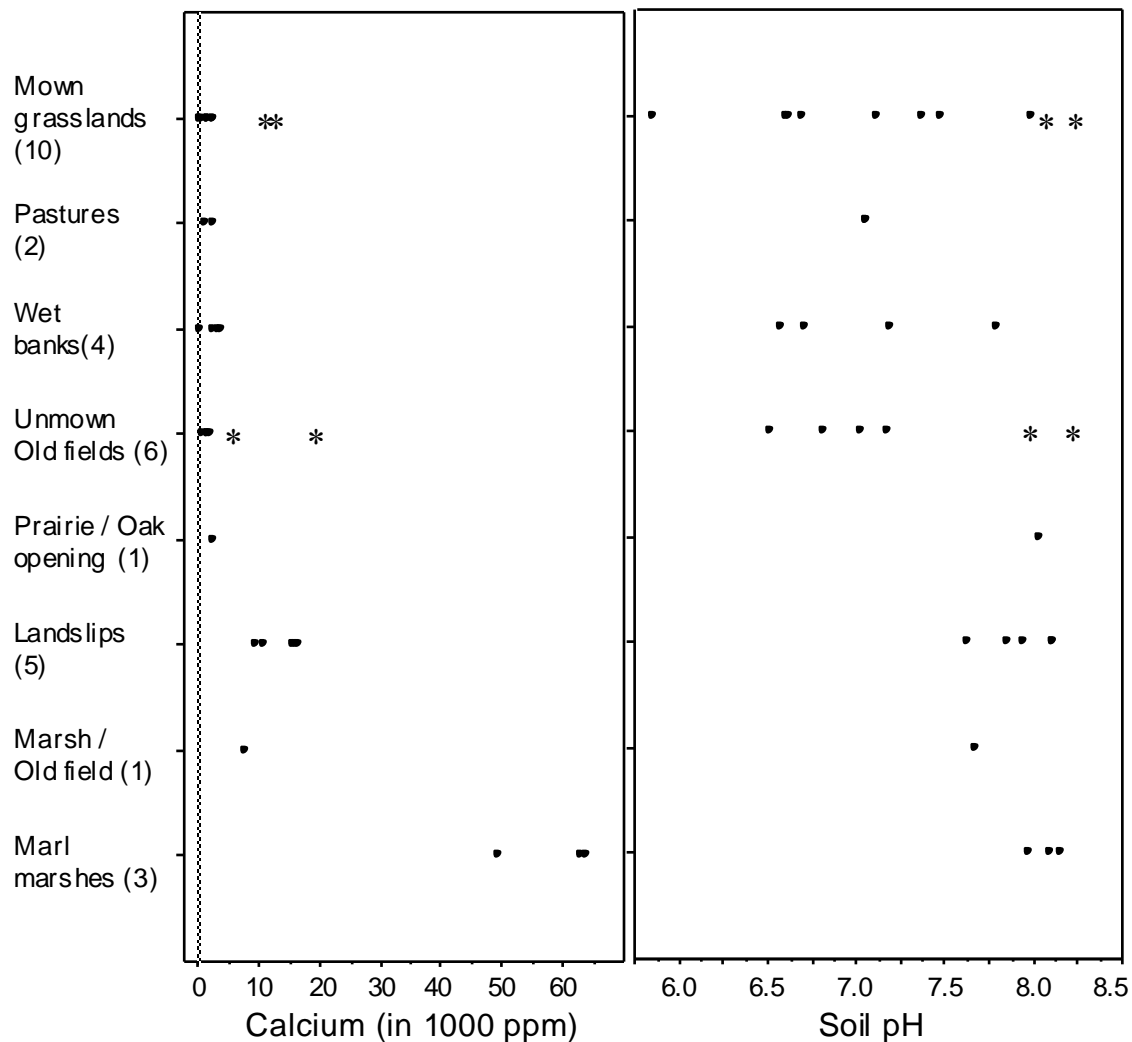


Fig. 5.3. Calcium content and pH of the soil at 32 sites where *G. crinita* was found (number of sites of each type shown in parentheses). Mown grasslands, pastures, and wet banks were managed. Four sites in addition to landslips with evidence of the subsoil having been heavily disturbed are shown as asterisks (*).

Particle size distribution and soil moisture indices

Few sites had particularly sandy or clayey soils; most had a more balanced proportion of particle sizes and relatively high silt percents (Fig. 5.4). Both these features are associated with high available water levels, as explained above. When classified according to the available water index, most sites fell into classes 4 or 5 (8 and 18 sites, respectively), on Etherington's (1982) scale in which 6 is wettest. Of the six sites in the lower available water classes (i.e. 1 and 3), none showed signs of waterlogging, but three were associated with ditches or seeps and probably had a good local supply of free-moving water. Sites were more evenly distributed between the three classes of the waterlogging index. Ten sites had waterlogging in the upper 5 cm, 10 had waterlogging below 5 cm, and 12 had no sign of waterlogging. However, when compared to the available water index classification, 6 of these 12 had relatively high available water indices, and 3 of the remaining 6 were associated with a local water supply as described above. Overall it seemed that *G. crinita* was not restricted to poorly drained situations but was generally associated with soils that had a high available water content.

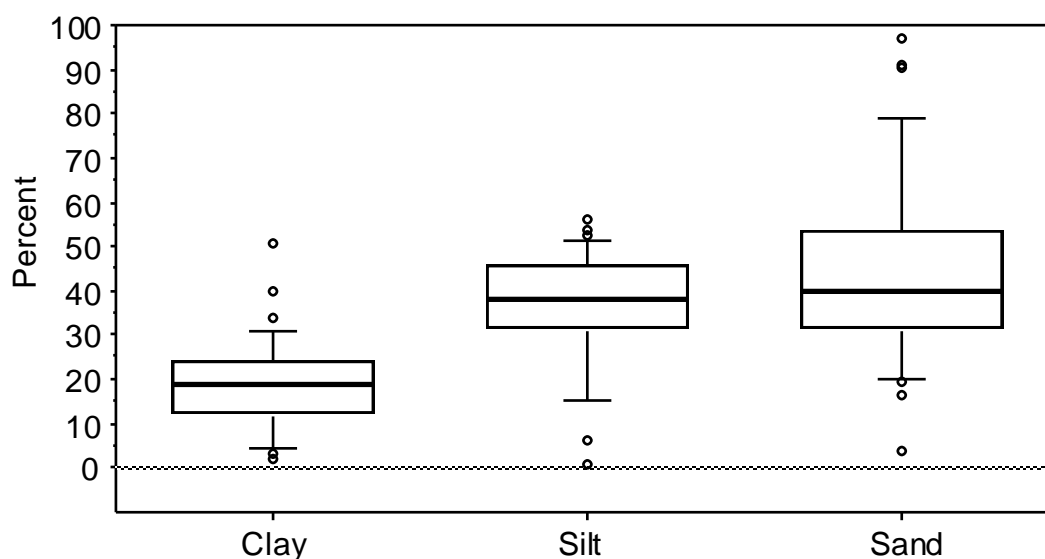


Fig. 5.4. Particle size distributions for soil from the rooting zone of *G. crinita* at 32 sites, showing the median value for all sites (horizontal line), quartiles (box), 10th and 90th percentiles (vertical line), and < 10th or > 90th percentiles (dots). Particle sizes follow the American system: clay is < 0.002 mm, silt is 0.002-0.05 mm, and sand is > 0.05 mm.

Population size

Only two sites, the Radio Lab and the Letchworth landslip, had more than 1000 flowering plants (Fig. 5.5). The survey sites covered a wide geographic range in New York State (Fig. 5.1) and had a variety of edaphic and topographic conditions so the population figures should represent a reasonable picture of the distribution of relative population sizes. However this picture is only a snapshot view as numbers will fluctuate from year to year, not necessarily in synchrony, depending on regional weather patterns and local site conditions. There is little available information on long term fluctuations in *G. crinita* populations, but the records that do exist suggest that population sizes greater than a few thousand probably rarely occur in New York State sites. Data (unpubl.) collected by D. Bassett (Naturalist for Letchworth State Park) for 2 sites in Letchworth State Park indicated that numbers varied by about 1000 or 2000 flowering individuals over a 5 year period, but numbers were usually less than 1000 (4 years out of 5 for one site, 2 years out of the 3 years with records for the other site). Along the roadside adjacent to the Fringed Gentian Natural Area near Ithaca, population sizes of flowering plants were less than 1000 for 3 years out of the 4 years with records, over the 5 year period 1985-1989 (pers. obs.).

Relative abundance: Density of plants

Density values calculated in relation to the entire extent of the population were low for most sites (Fig. 5.5), even though most populations were very limited in spatial extent. Three quarters of the sites were less than 0.3 ha in area. To see if relative abundance, as measured by density, was related to any of the soil chemistry or plant cover factors, Spearman rank correlations were made between density values and these factors. Few significant correlations were found (most p values were > .05). One significant correlation was found between magnesium and density ($p = .005$, $\rho = -.529$). Soil factors tended to correlate with each other, for instance calcium, magnesium and manganese were correlated with each other (Table 5.3), and correlations with several variables would be expected if a strong pattern were present. Given the high number of correlations between density and other factors that were tested (17), one or two significant correlations might arise by chance, so probably not much

importance should be attached to the magnesium and density result without further study. Kruskal-Wallis tests of density differences within the classes of soil moisture indices detected no significant differences ($p > .05$).

The assumption that conditions within an area occupied by a population are relatively homogeneous may not be accurate. In only 10 out of 29 sites were the plants subjectively considered to be distributed fairly evenly throughout, rather than being in patches of unequal densities. While the site survey illustrated the range of habitats and soils that were associated with *G. crinita* populations, investigation of the patterns of *G. crinita* distribution and abundance within sites was needed to more fully understand what conditions particularly favor or limit the survival of individuals. A detailed examination of how a patchy distribution within a site might reflect differences in survival is the subject of Section II.

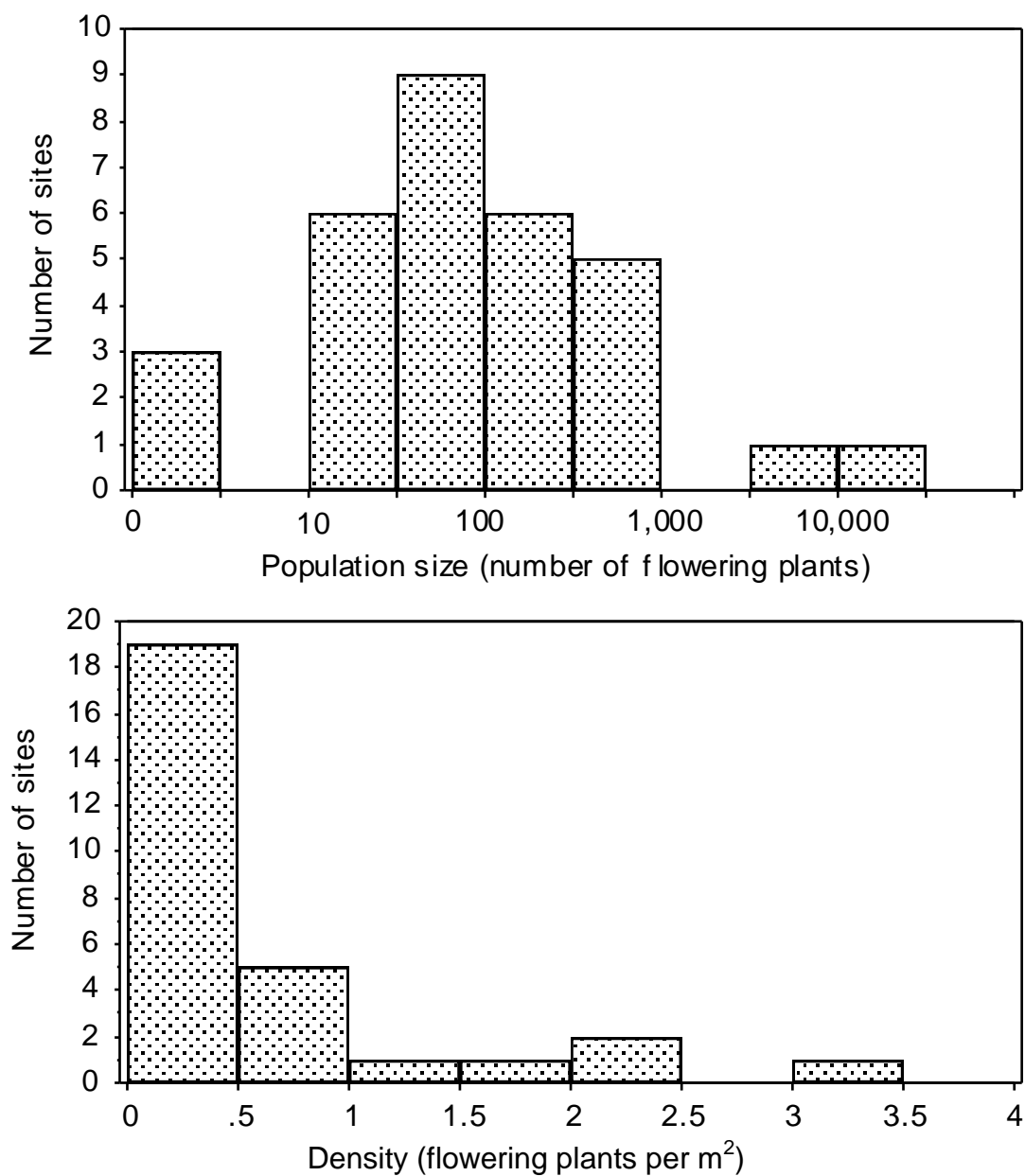


Fig. 5.5. *G. crinita* population size (number of flowering plants) and density (number divided by the total area) at 32 sites surveyed in September or October 1989. Two sites with only one plant flowering that year, and one site with none, are not included in the density figure.

Table 5.3. Correlation matrix of Spearman rank rho values, from 32 soil samples collected at *G. crinita* sites during September and October 1989.

	pH	Organic matter	P	K	Mg	Ca	Fe	Al	Mn
Organic matter	ns								
P	.445	ns							
K	-.442	ns	ns						
Mg	.417	.368	.405	ns					
Ca	.837	ns	.541	-.358	.616				
Fe	ns	-.484	ns	ns	ns	ns			
Al	-.408	ns	-.512	ns	ns	-.354	.645		
Mn	.606	ns	.405	ns	.635	.754	.413	ns	
Zn	ns	ns	.503	ns	ns	ns	ns	ns	ns
Absolute values of rho									
			> .35 are significant at		$\alpha = .05$				
			> .48		$\alpha = .01$				
			> .60		$\alpha = .001$				
			> .70		$\alpha = .0001$				

Reproductive performance

The flowering plants at the survey sites generally had only one or two flowers. Overall the median number was 2 flowers per plant (range 1-8) and 23 sites out of 31 had median numbers of 1 or 2 (1 at 12 sites, 2 at 11 sites). Median height of flowering plants at individual sites ranged from 9.5 to 34.5 cm, and the overall median height across the 31 sites was 18.3 cm. As might be expected, taller plants had more flowers. Median number of flowers per plant at each site was significantly correlated with median height (Spearman Rank Correlation, $p = .001$, $\rho = 0.595$, $n = 31$). However height and flower number are not simply interchangeable as measures of reproductive performance. Numbers of seeds per capsule were not sampled during the site survey, but results described in Chapter 4 for the Radio Lab site suggest that taller plants may also have more seeds per capsule. Therefore correlations were made between soil factors or plant cover and the flower number or height of *G. crinita* plants.

Some sites appeared to have been mown at some time during 1989. Depending on timing, mowing might sometimes lead to an increase in number of flowers rather than a decrease. Results already described in Chapter 4 show that loss of the top of the stem of second-year *G. crinita* plants can be associated with an increase in the number of flowers. Given the uncertainty about the effects of mowing, two separate analyses were made of the relationships between soil and plant cover factors

and reproductive performance as represented by number of flowers and height. Correlations (Spearman Rank) were tested for (a) sites apparently unmown in 1989 (n=24), and (b) all sites whether mown or not (n=31). The results for (b) should be treated with some caution but generally were similar to those for (a).

Despite the small range in median number of flowers among sites, some significant correlations were found. At unmown sites, number of flowers was significantly negatively correlated with percent clay content, pH, calcium, and manganese levels of the soil. Number of flowers was also negatively correlated with amount of moss cover on the ground (Table 5.4). The more "noisy" data set for all sites again showed negative correlations with calcium, manganese and moss cover (Table 5.4). In addition number of flowers was positively correlated with cover of tall herbs (i.e. plants ≥ 25 cm). Height of flowering plants was also positively correlated with amount of tall herb cover, for both unmown and all sites, but was not correlated with any soil factors (Table 5.4).

Table 5.4. Significant rank correlations between soil factors and plant cover and measures of reproductive performance across a range of sites in New York State.

	<u>Unmown sites (n = 24)</u>		<u>All sites (n = 31)</u>	
	p value	rho	p value	rho
<u>Flower number</u>				
Percent clay	.04	– .421	ns	--
pH	.04	– .428	ns	--
Calcium	.008	– .552	.04	– .377
Manganese	.02	– .479	.04	– .372
Moss cover	.02	– .492	.03	– .406
Tall herb cover	ns	--	.03	.387
<u>Height</u>				
Tall herb cover	.01	.52	.001	.596

The relationship between reproductive performance and soil moisture was analyzed by using Kruskal-Wallis tests to examine differences in flower numbers and height in (a) waterlogging index classes and (b) available water index classes. Neither plants in unmown sites nor in all sites had significantly different flower numbers in the three waterlogging index classes ($p > .05$). However in both groups of sites, flower numbers were significantly different among available water classes ($.025 < p < .05$). It should be noted that numbers of sites in each class were rather variable, and low in some classes.

Available water class:	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>
Number of unmown sites	0	0	3	6	15
Number of all sites	3	0	3	7	18

Multiple comparisons of means (Conover 1980) indicated that for both data sets, plants from sites in class 3 had more flowers than those in class 5 (a wetter class) though other comparisons between classes were not significant ($p > .05$).

Median heights of plants at the sites in the three waterlogging index classes were not different. Among available water index classes, height was only significantly different between classes when all sites were considered ($.025 < p < .05$). Multiple comparisons of means revealed that class 1 (driest) had significantly smaller plants than class 3 ($p < .05$).

To attempt to confirm the differences in reproductive performance found in the site survey, the pattern of reproductive performance in relation to soil factors and cover of other plants was studied within a site (the Radio Lab field) and the results are discussed in Section II.

Summary of Section I

Populations of *G. crinita* were associated with open, unwooded habitats in New York State. Sites were generally on more or less level terrain and often had a history of natural disturbance or human disturbance and management. However *G. crinita* was mostly found in localities that were well-vegetated rather than areas with sparse plant cover. Soils were usually neutral to alkaline and high pH and calcium levels tended to be found in sites which had evidence of past or present soil disturbance. Sites frequently had soils that had high available water content and/or poor drainage. Between sites, the relative abundance of *G. crinita*, measured by density of plants, was not correlated with varying levels of most soil factors or plant cover. However relative reproductive performance was related to some of these factors. Plants tended to have more flowers in sites with lower pH and calcium levels and were taller where tall herbs formed a greater part of the vegetation. Flower number and plant height appeared to be greater in sites with soils that had moderate amounts of available water.

SECTION II. PATTERNS OF DISTRIBUTION, ABUNDANCE, SURVIVAL AND PERFORMANCE OF *Gentianopsis crinita* WITHIN A SITE

To investigate the patchiness of *G. crinita* within a site and how distribution, abundance, survival and performance might relate to soil factors, plant cover and herbivory, detailed studies were carried out at the Radio Lab site. Preliminary work in 1987 and 1988 showed that the population there was patchily distributed, and that survival varied across the field. In addition some evidence was collected about factors that might influence these patterns. In 1989, these studies were followed up by investigating factors associated with patchiness of *G. crinita* along a transect and in 2 transplant experiments. The rationale for the choice of these methods was based on the results of the preliminary work.

Preliminary studies

During the autumn of 1987, it had become clear that flowering *G. crinita* were patchily distributed in the Radio Lab field (Fig. 5.6). A similar pattern was seen in 1988 (Fig. 5.7). In contrast, flowering *D. carota* appeared to be widely distributed, although with areas of higher abundance, generally where *G. crinita* densities were lowest (Figs. 5.6, 5.7).

However, seedlings of *G. crinita* were found to be able to emerge and survive across the whole field during the 1987 growing season. In the spring of 1987, the presence or absence of seedlings of both species was recorded from 60 randomly located 20 by 20 cm plots in a 50 x 30 m area within the field, for a study of regeneration in different microhabitats (Chapter 3, Section II). Twenty of the 60 plots had been sown with *G. crinita* seeds, and 20 with *D. carota* seeds, in the autumn of 1986. *G. crinita* seedlings emerged in all 20 sown plots, and plants survived through to the last census of the year in November 1987. Twelve of 40 unseeded plots also had *G. crinita* seedlings, and plants survived in all plots except one (Fig. 5.8a). *D. carota* seedlings emerged in all the seeded plots and survived in all except one plot. Again, the species was more ubiquitous than *G. crinita* as it occurred in all 40 of the unseeded plots (Fig. 5.8b).

The success of *G. crinita* (emergence from sown seed, and survival) throughout the field did not continue in 1988. Survival in existing plots was monitored, and seedling emergence and survival in an additional 30 seeded plots (15 of each species) were also recorded (Chapter 3, Section II). From the end of May into the first week of July, the Ithaca area suffered a drought which is described more fully in Chapter 2. Many *G. crinita* plants died during this time, both seedlings and older plants, after first wilting then shrivelling. In seeded plots, mortality of both seedlings and second-year plants was 89% over the period May through November 1988. The pattern of survival in plots was markedly different from 1987 (Fig. 5.8c,e), with survival concentrated in the southern part of the field, parallel to the course of the seasonally active water channel. During the project water was observed to flow eastwards along this channel during spring and autumn and in wet periods in summer, and puddles of standing water appeared near the channel after wet weather. Mortality of *D. carota* seedlings was high during the drought (87% in seeded plots), but plants over 1 year old had lower mortality (67% in seeded plots) and the spatial distribution of survivors remained wider than for *G. crinita* (Fig. 5.8d,f).

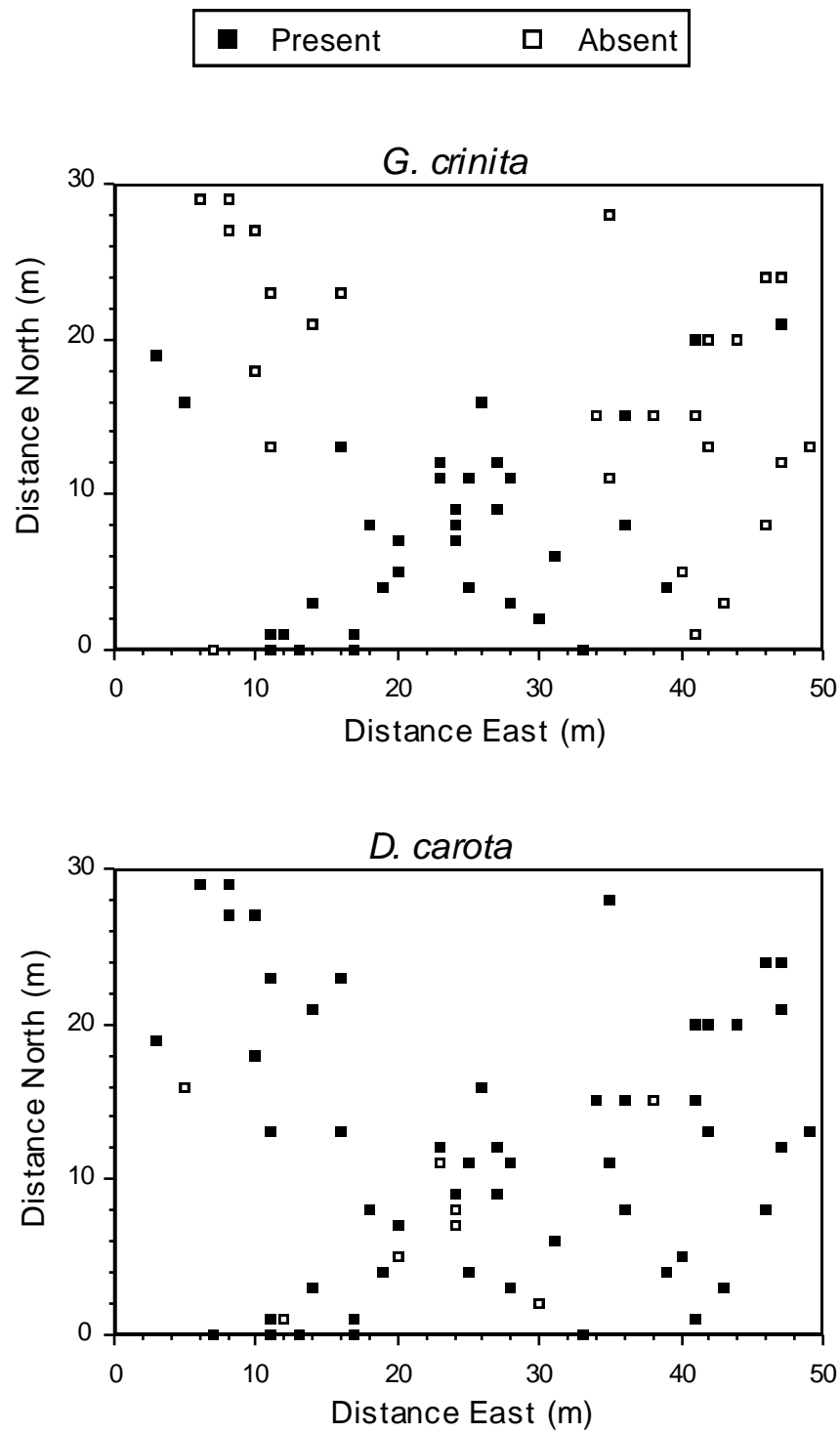


Fig. 5.6. Spatial distribution of flowering *G. crinita* and *D. carota* across the Radio lab field in September 1987, sampled in 60 random plots (1 m by 1 m).

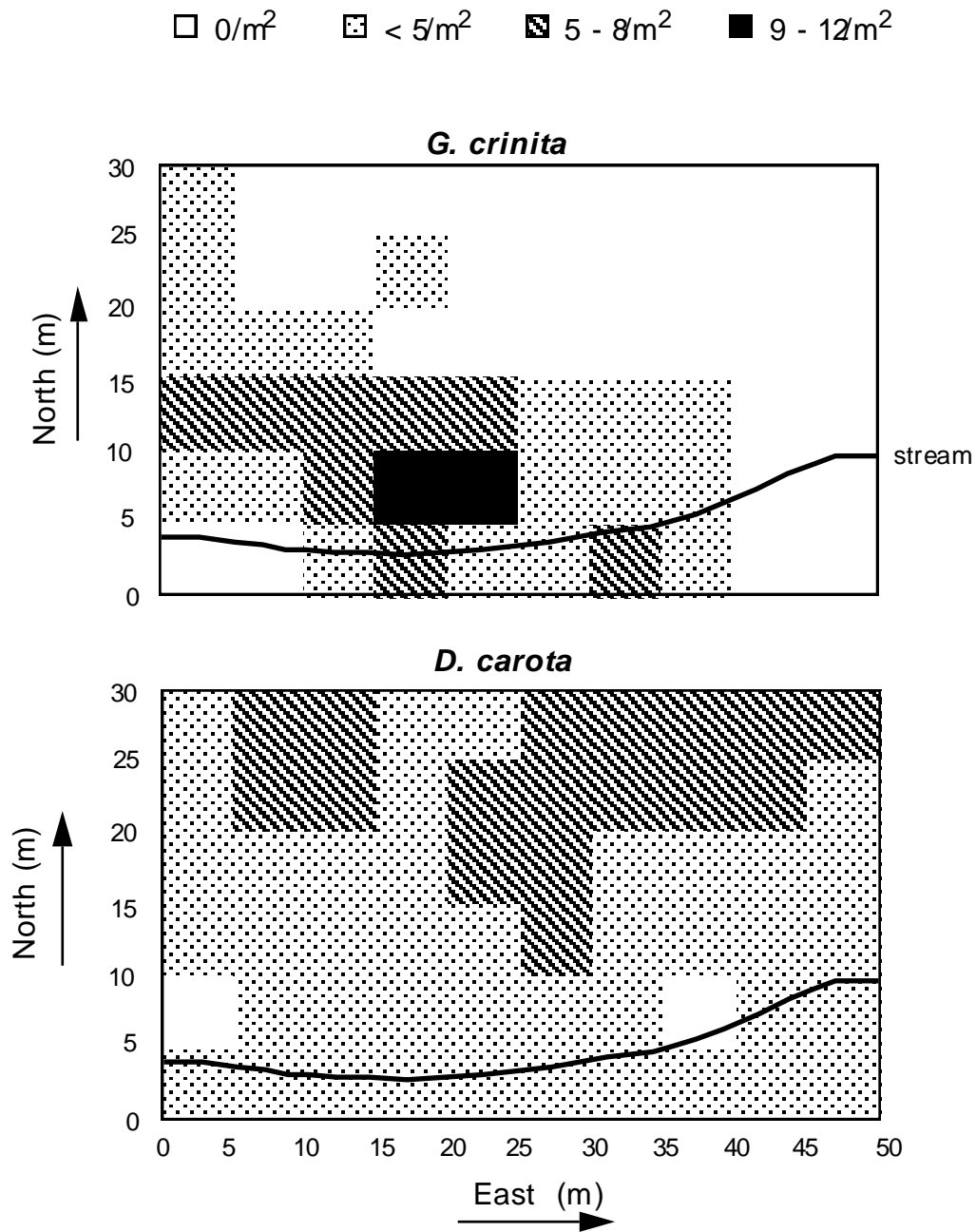


Fig. 5.7. Spatial distribution of flowering plants of *G. crinita* and *D. carota* at the Radio Lab field in September 1988, from the average density in 4 plots (1 x 1 m) in the corners of each 5 x 5 m grid square, shown relative to the seasonal stream channel.

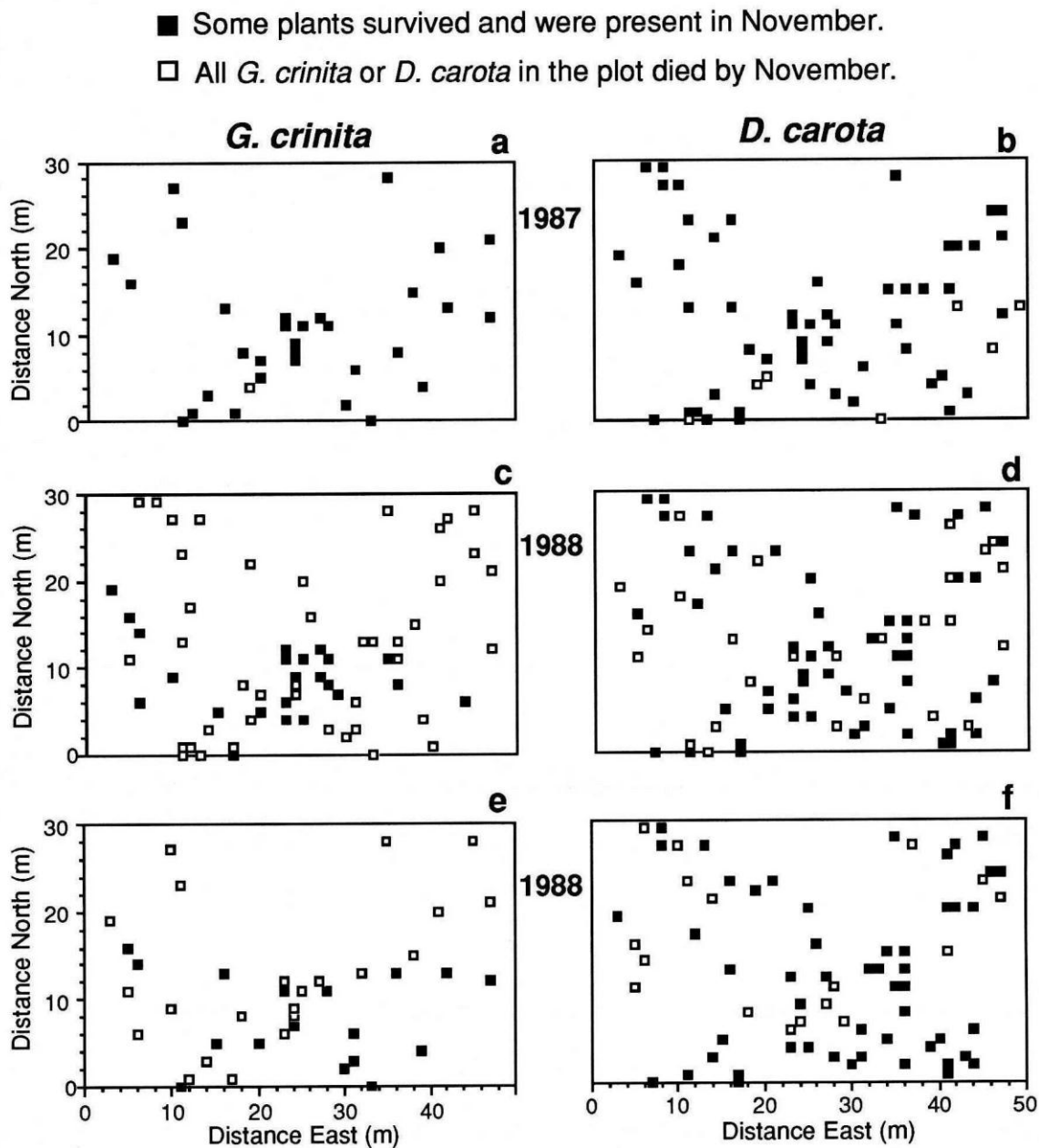


Fig. 5.8. Spatial distribution of survival at the Radio Lab field, in randomly positioned 20 by 20 cm plots (a total of 60 plots in 1987, 90 in 1988) which contained *G. crinita* and/or *D. carota*, including naturally occurring plants and ones from sown seed (plots without either *G. crinita* or *D. carota* at the beginning of each growing season are not shown). Plot size is not shown to scale. Survival of plants in areas other than within plots is not shown.

a, b) Seedling survival from May to November in 1987; n = 32 plots with *G. crinita*, 60 plots with *D. carota*.

c, d) Seedling survival from June to November in 1988; n = 65 and 79 plots.

e, f) Survival of plants >1 year old from June to November in 1988; n = 39 and 69 plots (including any 1987 plots with survivors to 1988, and those in 30 additional plots).

Some supporting evidence for the association of *G. crinita*'s survival with a soil moisture gradient came from soil moisture tension data collected in May, June and August 1988. Two readings were made with a Model 2900F Soil Moisture Probe (Soilmoisture Corp.) at 5 cm depth, at the northwest and southeast corners of the 30 plots (20 by 20 cm) seeded in 1988. Each reading was made 1 minute after inserting the probe into the soil, and the two readings from each plot were averaged. At the end of May, the wetter plots were primarily in the southern part of the field (Fig. 5.9). By the end of June the upper 5 cm of soil in previously moist plots had become drier and more similar to other plots elsewhere in the field (Fig. 5.9), but rainfall in July and August re-established a pattern similar to that in May. These results suggest that the southern part of the field may have had more moisture present through the soil profile as a whole, which could therefore be more quickly "topped up" after rainfall.

As well as spatial differences in abundance and survival of *G. crinita* in the Radio Lab field, it was found that performance, measured by the diameter of the rosette at the end of the first season's growth, was an important factor influencing overwinter survival and subsequent reproductive output. As part of a study of the regeneration of *G. crinita* in different microhabitats (described in Chapter 3, Section II), 322 marked rosettes were measured in November 1988. Significantly more of the larger plants survived into May 1989 compared to the smaller plants ($\chi^2 = 43.27$, $p = .0001$, median rosette diameter dividing "large" and "small" plants = 11 mm). Similarly, of 222 *D. carota* first-year rosettes, more larger plants survived than smaller individuals ($\chi^2 = 23.54$, $p = .0001$, median rosette diameter = 30 mm). For both species data from plants in different microhabitats were pooled as there were no differences in survival between microhabitats. Subsequently it was found that size of first-year *G. crinita* rosettes also influenced number of flowers that they produced in the second year. Size in November 1988 of first-year plants was significantly correlated with number of flowers produced by the survivors among these plants in September 1989 (Spearman Rank Correlation, $p < .00001$, $\rho = 0.53$, $n = 74$).

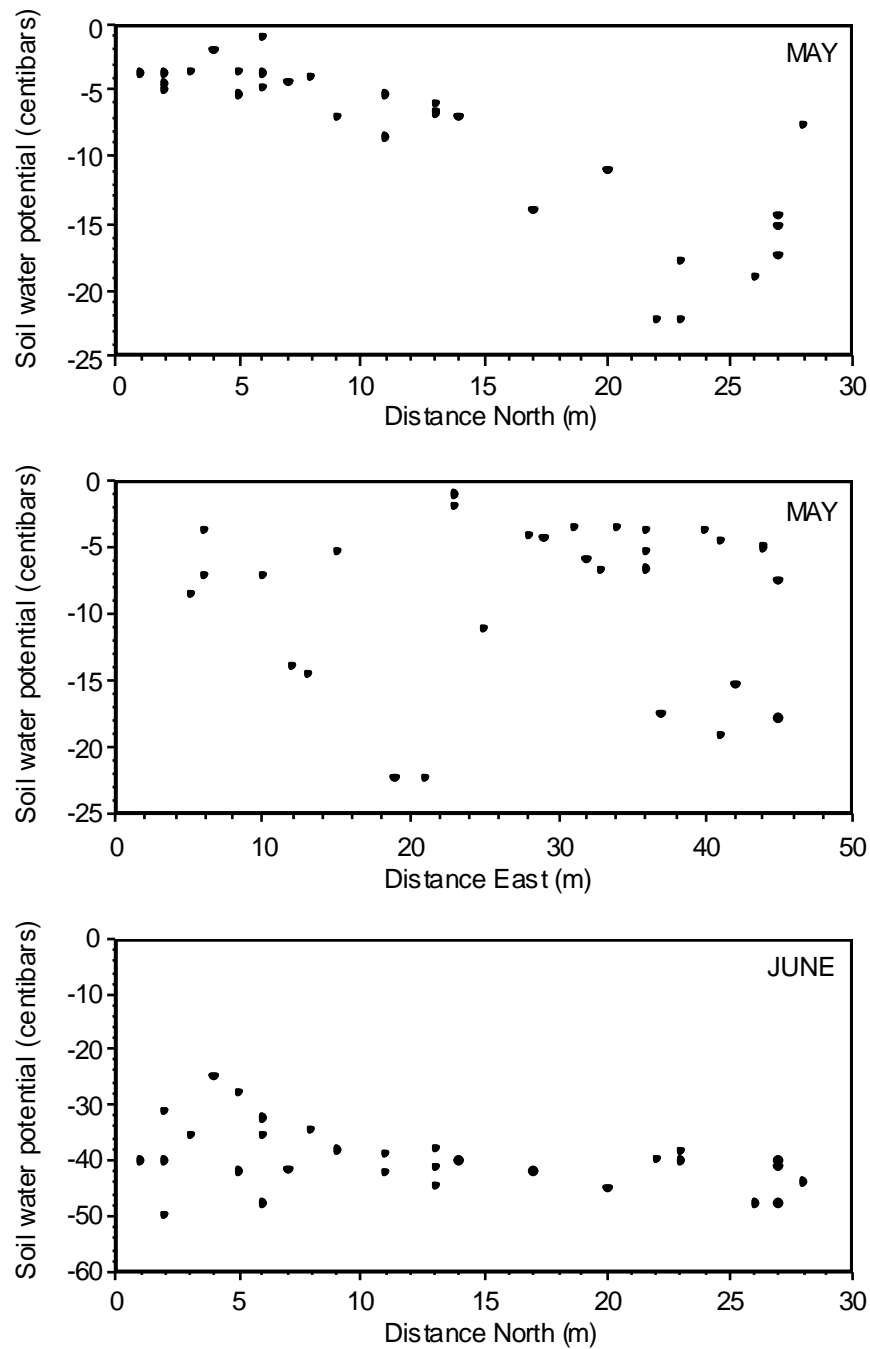


Fig. 5.9. Variation in soil water potential with distance across the Radio Lab field in 1988, measured in 30 random plots on 31st May and 20th June. Values are shown for the north-south and east-west axes of the field in May and for the north-south axis only in June. The east-west axis had a similar pattern to that shown for May.

Transect study

Materials and Methods

Given the distribution and survival pattern of *G. crinita* in the Radio Lab field and the possibility of a north-south soil moisture gradient being one important factor, I decided to lay out a 30 m long transect across the 50 x 30 m area in the field from south to north in spring 1989. The transect was at approximately the midpoint along the east-west axis of the field (21 m from the west edge, to avoid existing plots). Every 1 m along the transect, a 40 by 80 cm quadrat was laid out with the long side east-west. In two other transects, laid out at 10 and 35 m from the western edge of the field, while the pattern of *G. crinita*'s distribution was the same, numbers of individuals per quadrat were much lower, making the detection of perhaps subtle differences in density in relation to environmental and biotic factors a difficult task at this scale. Effort was therefore concentrated on the transect at 21 m.

In early June 1989 (7-10th) the numbers of seedlings and plants older than one year of both species were recorded in each quadrat. Estimates of vascular plant cover, amount of bare ground and moss were made by eye using a grid divided into 200 4 cm by 4 cm squares. Between 2nd and 7th July, 50 seedlings of each species were randomly selected and marked in each of 3 density classes: < 25 plants per 40 x 80 cm quadrat ($n = 56$ for *G. crinita* in this class), 25-149 per quadrat, and ≥ 150 per quadrat. Survival was followed by censusing marked seedlings in August (24-31st) and November (8-11th). Estimates of chewing damage were also made at these dates. Performance during the first year was measured by recording rosette diameter of survivors in November. Numbers of remaining plants older than one year were also recorded in November. In September (18, 19th) flowering plants of *G. crinita* were sampled along the transect to measure reproductive performance. Height to the base of the uppermost flower was measured and number of heads (buds through to seed capsules) was recorded. If fewer than 50 plants occurred in a quadrat then all were measured, if more than 50 were present, a random sample of 50 was chosen.

The spring of 1989 was wet (Chapter 2; Fig. 2.6) and the soil in the Radio Lab field was saturated into June. By July it had begun to dry out and readings of relative soil moisture tensions were made along the transect on 3rd July and 27th August. One reading from the center of each quadrat was made with the probe at 5 cm depth. The probe was left in the ground for a longer period (5 min.) than for previous readings (1 min. in 1988), in case more time was necessary to pick up small differences in tension, although measurements made after 1 and 5 minutes in 8 trials showed the same relative differences in soil moisture across the field.

Soil samples from the rooting zone were collected from each quadrat on 14th November 1989. A volume equivalent to six 10 cm deep cores were taken with a 2 cm diameter soil corer, along the east-west midline of each quadrat. After mixing, a subsample was sent to the Cornell Nutrient Analysis Laboratories and the same range of analyses was done as described in Section I. A further subsample was refrigerated and the pH of this moist soil was measured on 4th December 1989 with a Beckman portable pH meter using a 1:1 soil/distilled water suspension.

Data analysis

Data were analyzed by non-parametric Spearman rank correlation to assess the association between the abundance of the two species per quadrat and the soil factors and plant cover, because these data were not normally distributed. As the number of correlations made was high, some may have arisen by chance. However, as strong, consistent patterns were evident, all significant correlations are reported.

Survival and herbivory data in the density classes were analyzed by χ^2 tests of association. The following categories were used to visually estimate the amount of chewing damage on first-year

plants: I. < 10%, II. 10 to 49%, III. 50 to 74%, IV. \geq 75%. These estimates were somewhat rough but estimation was made easier by the fact that petioles or bases of leaves of both species were often left unchewed, showing where leaves had recently been lost.

Results

Distribution and abundance

The difference in distribution of the two species, which had been observed in previous years, was confirmed by the transect study. The pattern at June 1989 is shown in Fig. 5.10. *G. crinita* was concentrated at the southern end of the transect while the abundance of *D. carota* peaked towards the northern end. *G. crinita* was not present at all in several quadrats in the northern end of the transect, but all quadrats contained *D. carota* (Fig. 5.10). For each species, the two generations, i.e. seedlings and older plants, showed very similar distributions (Fig. 5.10).

As there may have been a slightly smaller element of chance in the distribution of the older plants, which had been exposed to potentially selective environmental conditions over a longer period than seedlings, correlations with environmental factors were made using a census of older plants. June was chosen arbitrarily but in fact the June and November distributions of older plants of both species were closely correlated (*G. crinita* $\rho = .982$, $p < .0001$; *D. carota* $\rho = .872$, $p < .0001$). *G. crinita* was actually present in greater numbers than *D. carota* but the transect was located across a particularly "good" area for *G. crinita* (Fig. 5.7).

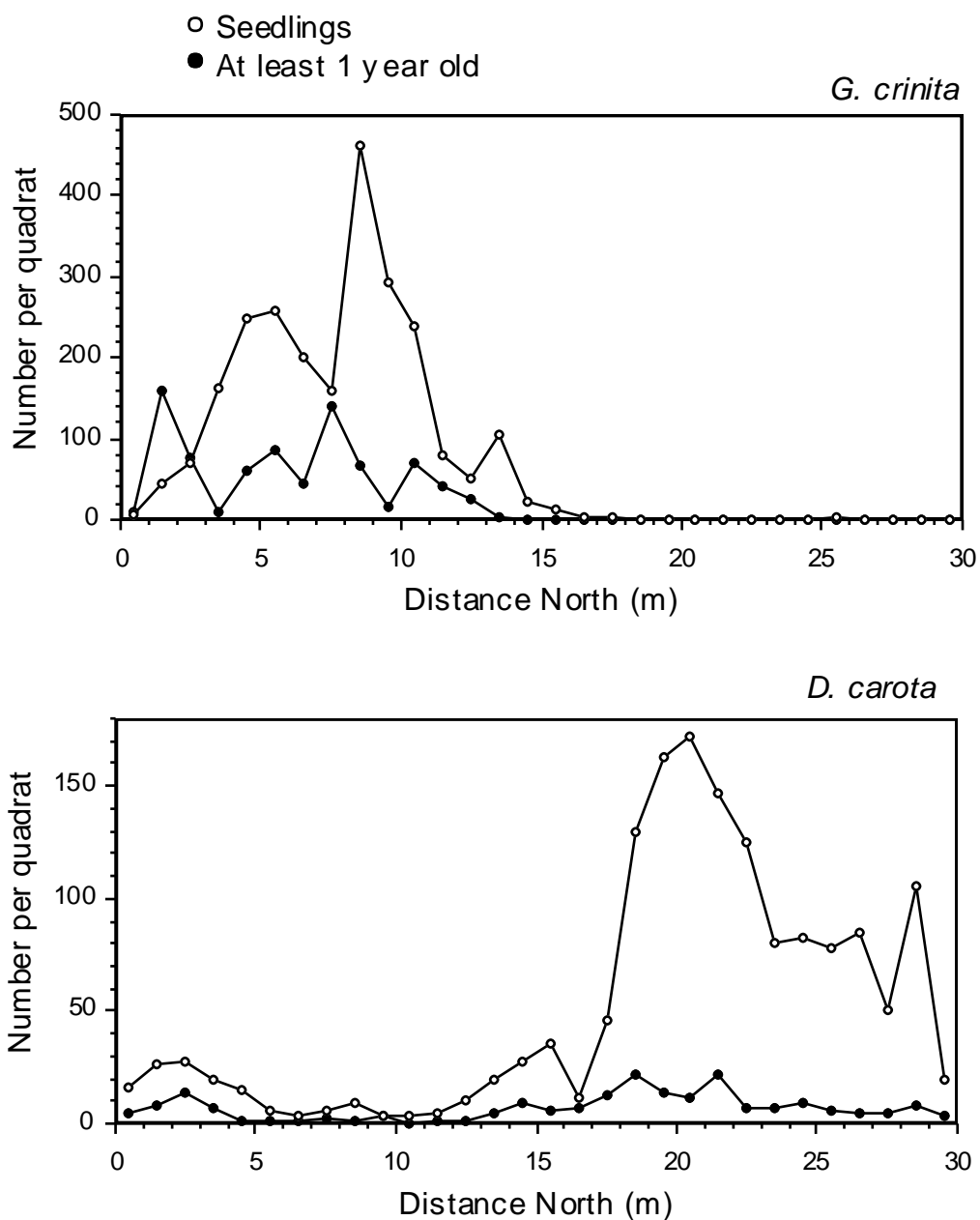


Fig. 5.10. Distribution and abundance of seedlings and plants over 1 year old, of *G. crinita* and *D. carota* (note difference in scale) in quadrats along a 30 m transect across the Radio Lab field (7-10 June 1989). Quadrats measured 40 cm (N-S) by 80 cm (E-W) and were spaced every 1 m along the transect.

Levels of many of the environmental factors showed similar patterns along the transect, particularly among the soil chemistry factors. Calcium, magnesium, manganese, and pH (measured on dry soil) were all strongly positively related (Table 5.5) and were highest at the southern end of the field (e.g. pH and calcium; Fig. 5.11). Some factors showed the opposite kind of distribution, with highest levels at the northern end of the field, particularly potassium (Fig. 5.11). This factor had a strong positive correlation with loss on ignition (an index of organic matter content) and negative correlations with the 'calcium group' of factors (Ca, pH, Mg, Mn; Table 5.5). Given the similarity between the levels of the calcium group factors and abundance of *G. crinita* across the transect, and the potassium group with *D. carota* (Figs. 5.10, 5.11) it is not surprising that *G. crinita* showed positive correlations with the calcium group and negative correlations with potassium and organic matter; the reverse was the case for *D. carota* (Table 5.5). Out of all the soil factors measured, only phosphorus was not significantly correlated with either species.

The correlations with pH need to be treated with some caution. The measure of pH on moist soil as compared to dry soil also was positively correlated with *G. crinita*'s abundance, but not with *D. carota* (Table 5.5). As discussed in Section I, pH of alkaline soils may vary depending on soil moisture level. Actual pH experienced by the plants during wet periods may be more like values measured on moist soil samples, while in dry conditions a pattern more like that resulting from dry samples may obtain (Fig. 5.11c).

The pattern of relative soil moisture across the transect was similar in June and August (Fig. 5.11), and as expected in both months *G. crinita* abundance was negatively correlated with soil moisture tension, i.e. it was more abundant in the moister southern end of the transect, while *D. carota* was positively correlated, i.e. it was more abundant in the drier northern end of the transect (Table 5.5).

G. crinita was more abundant where amount of plant cover was lower, while *D. carota* showed the opposite pattern (Table 5.5). However, the effect of competition, as represented by plant cover, and the influence of soil conditions cannot readily be disentangled as the two are themselves related. The relative amounts of plant cover may be influenced by soil nutrient levels and in turn can affect soil conditions, for example by increasing soil organic matter content. In fact plant cover in June was positively related to loss on ignition (an index of amount of organic matter in the soil; Fig. 5.12; Spearman rank correlation, $p = .004$, $\rho = .535$). Greater plant cover (Fig. 5.12) was also associated with high potassium ($\rho = .683$, $p = .0002$) and low calcium ($\rho = -.656$, $p = .0004$). However, amount of plant cover was not correlated with soil moisture levels in June or August.

Amount of moss and bare ground cover were not related to *G. crinita*'s abundance ($p > .05$); but moss cover was positively related and bare ground was negatively related to *D. carota*'s abundance (moss: $\rho = .46$, $p = .009$; bare ground: $\rho = -.392$, $p = .035$). This contrasts with results of seed sowing experiments (Chapter 3, Section II) where both species were found to favor moss and bare ground microhabitats for regeneration. The high proportion of bare ground where *D. carota* abundance was low (Figs. 5.10, 5.11) suggests that some deleterious factor was overriding the availability of favorable microhabitat, perhaps the high soil moisture levels in wet years (see Section III).

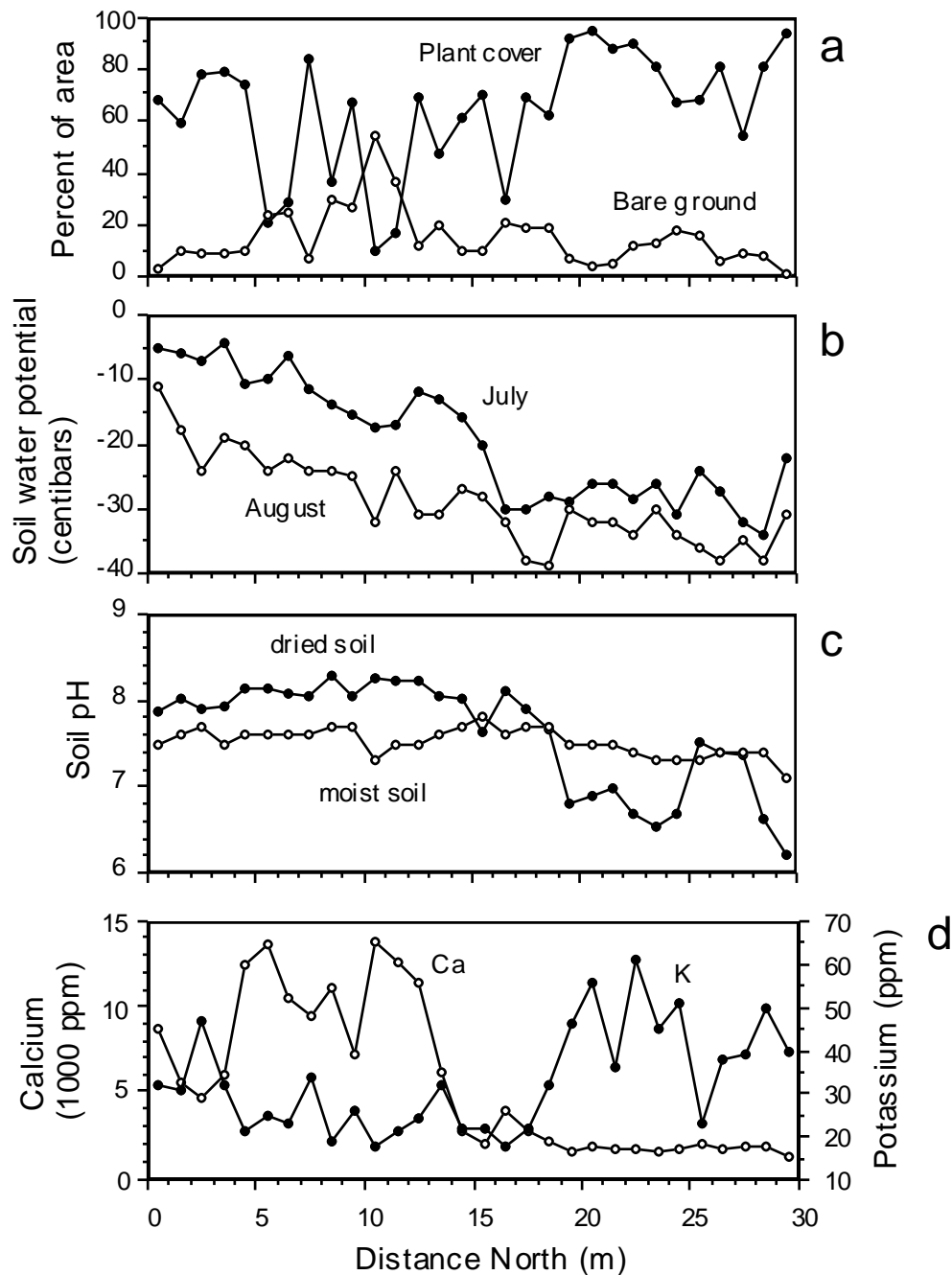


Fig. 5.11. Variation in quadrats 1 m apart along a 30 m transect across the Radio Lab field in 1989, in:

- a) plant cover and bare ground (7-10 June),
- b) soil moisture content expressed as soil water potential, i.e. the negative equivalent of soil moisture tension (3 July and 27 August),
- c) soil pH (for moist soil and for dry soil), and
- d) available calcium and potassium.

Soil samples for pH and nutrients were collected from the rooting zone of *G. crinita* in November.

Table 5.5. Correlation between soil factors within the Radio Lab field, and between soil factors or plant cover and abundance of *G. crinita* or *D. carota* (in June 1989), along a 30 m transect across the field (n = 30 samples, from 40 by 80 cm quadrats spaced 1 m apart).

	pH (dry)	Organic matter	P	K	Mg	Ca	Fe	Al	Mn
Organic matter	-.683								
P	ns	ns							
K	-.814	.691	ns						
Mg	.824	-.386	ns	-.600					
Ca	.930	-.624	ns	-.683	.862				
Fe	.391	-.608	ns	ns	ns	.523			
Al	ns	-.478	ns	ns	ns	ns	.801		
Mn	.799	-.654	ns	-.497	.751	.880	.762	.414	
Zn	ns	ns	.490	ns	ns	ns	.564	ns	.531

Absolute values of rho > .38 are significant at $\alpha = .05$
> .47 $\alpha = .01$
> .62 $\alpha = .001$
> .75 $\alpha = .0001$

Correlations between soil factors, plant cover, and density of plants > 1 year old, for each species:

	<i>G. crinita</i>		<i>D. carota</i>	
	rho	p value	rho	p value
pH (dry soil)	.805	<.0001	-.626	.0007
Organic matter	-.613	.001	.611	.001
Phosphorus	--	ns	--	ns
Potassium	-.460	.01	.503	.007
Magnesium	.709	.001	-.462	.01
Calcium	.856	<.0001	-.661	.0004
Iron	.628	.0007	-.593	.001
Aluminum	--	ns	-.467	.01
Manganese	.852	<.0001	-.647	.0005
Zinc	.475	.01	--	ns
Soil moisture				
July	-.796	<.0001	.436	.02
August	-.741	<.0001	.373	.045
Plant cover	-.482	.009	.437	.02
Moss	--	ns	.486	.009
Bare ground	--	ns	-.392	.035

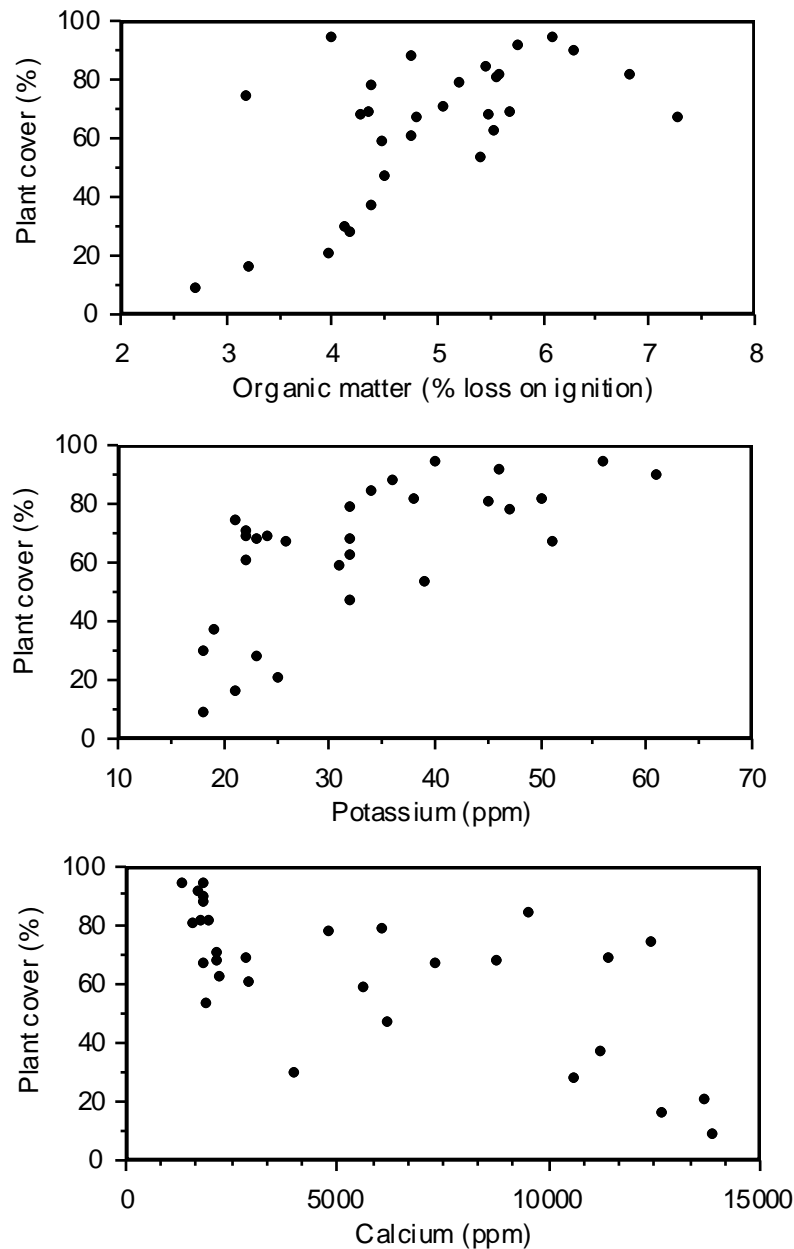


Fig. 5.12. Plant cover in relation to soil organic matter (% loss on ignition), available potassium, and available calcium, in 30 quadrats 1 m apart along a transect across the Radio Lab field in 1989. Plant cover was recorded 7-10 June, soil samples were collected in November.

Survival and performance

Among plants older than one year, *D. carota* had rather lower survival along the transect than *G. crinita*: in 31% of plots, < 50% of *D. carota* survived, compared to only 12.5% of *G. crinita* plots with < 50% survival, and > 70% of *G. crinita* plants survived in 62.5% of the plots, while only 17.2% of *D. carota* plots had at least 70% survival. Neither species showed any significant correlations ($p > .05$) between survival percents of older plants and environmental factors.

More of the marked *G. crinita* seedlings survived from July to November where their density was lower. *D. carota* showed the same pattern of low survival in dense areas (*D. carota*: $\chi^2 = 7.12$, $p = .03$;

G. crinita: $\chi^2 = 21.94$, $p = .0001$). The spatial distribution of 3 density classes across the transect, and their different survival percents, are shown in Fig. 5.13. Thus survival showed the opposite pattern to that which might be expected given the relative abundances of each species in different parts of the transect.

G. crinita seedlings in the lower density classes not only had higher survival but also grew larger. Rosette diameter in November 1989 was significantly different between the three density classes (Kruskal-Wallis $H = 65.09$, $p < .005$). Rosettes were largest (median diameter 57 mm) in the lowest density class and rosettes in the middle density class (median 24 mm) were larger than those in the highest density class (median 17 mm; Multiple comparison tests, $p < .05$). *D. carota* seedlings did not have significantly different rosette diameters in the 3 density classes in November 1989 (Kruskal-Wallis $H = 2.69$, $p > .05$). Median rosette diameters were: 38 mm in the low density class, 23 mm in middle density, and 38 mm in high density.

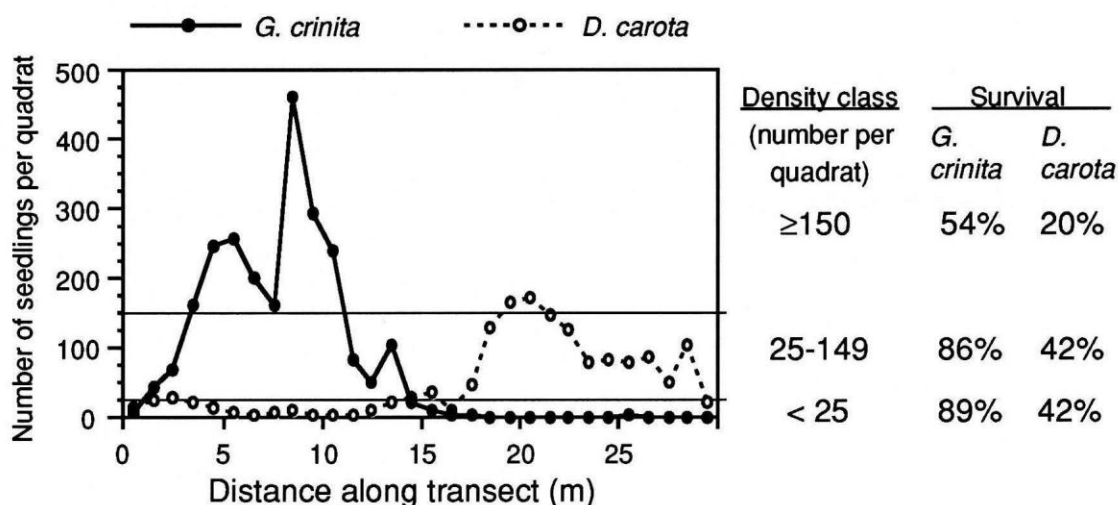


Fig. 5.13. Comparison of the spatial distribution and abundance of *G. crinita* and *D. carota* seedlings in quadrats, 40 by 80 cm, 1 m apart along a 30 m transect across the Radio Lab field (7-10 June 1989) together with the survival of marked seedlings from 2-7 July to 8-11 November 1989 in each of three density classes (equivalent to < 78 , 78-466, and > 466 per square meter). A random 50 seedlings of each species were marked in each class, except for the lowest density class of *G. crinita* where 56 plants were marked.

Herbivory

The incidence of herbivory, recorded in November 1989, differed between density classes for *G. crinita* ($\chi^2 = 8.78$, $.01 < p < .025$). More first-year *G. crinita* plants (82%) in the lowest density class (< 25 per 40 x 80 cm quadrat) showed evidence of chewing damage than plants in the other two classes (67% of plants at 25-149/quadrat, 50% at ≥ 150 /quadrat; $\chi^2 = 6.35$, $.01 < p < .025$). Although *D. carota* showed a similar pattern of incidence of chewing (60%, 40%, and 30%) the differences were not significant ($p > .05$). The lower overall proportions of *D. carota* damaged (46% of plants vs. 64% of *G. crinita*, $\chi^2 = 8.29$, $.01 < p < .025$) may merely reflect *D. carota*'s tendency to produce new leaves through the season as old ones senesce, so evidence of damage may have disappeared by November while leaves of *G. crinita* tend to remain green all season.

For each species, numbers of plants damaged by herbivory in each density class were too few to test the effect of the amount of damage on subsequent survival. When the classes were combined for *D.*

carota and damage categories III and IV pooled ($\geq 50\%$ damaged), an assessment of August survival in relation to amount of damage in July was possible. No significant association was found ($p > .05$). The majority of marked *G. crinita* seedlings in the combined density classes were in categories I and II ($< 50\%$ damaged) in July, and no significant difference was found in subsequent survival to August. Mortality was very low between August and November for both species, so no analysis of association of mortality in November with amount of damage in August was possible.

Reproductive performance

The production of flower heads by second-year plants was uniform along the transect. The median number of heads per plant was only 1 in every quadrat along the transect that contained second-year plants (16 quadrats). Out of a total of 385 plants measured, only 40 had more than one flower head. However data on seed numbers per capsule and height of a random sample of 60 plants in the Radio Lab field, recorded in 1989 (Chapter 4), showed that the number of seeds per capsule was closely related to the height of the plant (Fig. 4.3). Taller plants produced more seeds per capsule. Therefore median height of plants in quadrats along the transect was used as an indicator of relative reproductive performance and correlations with soil factors and plant cover were tested.

Median height was positively correlated with the organic matter index and potassium, and negatively correlated with pH (measured on dry soil), calcium, iron, aluminum and manganese (Table 5.6). Median height was not correlated with soil moisture, plant cover, moss cover, or bare ground. Amount of plant cover may primarily have represented the degree of interspecific competition. When intraspecific competition, represented by density of second-year plants, was tested against median height, again no correlation was found.

Table 5.6. Significant correlations between median height of *G. crinita* and soil factors along a 30 m transect in the Radio Lab field ($n = 16$ samples, from 40 by 80 cm quadrats spaced 1 m apart). Phosphorus, magnesium, zinc, soil moisture in July and August, plant cover, moss cover, and bare ground were not correlated with median height.

	rho	p value
pH (dry soil)	– 0.720	.005
Organic matter	0.528	.04
Potassium	0.591	.02
Calcium	– 0.643	.01
Iron	– 0.596	.02
Aluminum	– 0.640	.01
Manganese	– 0.667	.01

Seed transplant experiment

A seed transplant experiment was carried out in the 50 x 30 m area within the Radio Lab field in 1988-89 to investigate experimentally whether the patchiness of *G. crinita* was the result of better survival and growth in areas where its abundance was higher. In addition the experiment aimed to find out if *G. crinita* survived better than *D. carota* in these areas, and worse where it was less abundant. *D. carota* appeared to be generally most abundant where *G. crinita* was least abundant and vice versa.

Methods

Seeds of both species were introduced into areas which had high and low abundance (i.e. density) of adult plants of the 2 species in the fall of 1988. From the grid map that showed the distribution of flowering *G. crinita* and *D. carota* in 1988 within the field (Fig. 5.7) the five 5 by 5 m squares with the highest densities of each species were identified in fall 1988. *D. carota* was more abundant in the north part of the field and *G. crinita* in the south part of the field. In the center of each square, two 20 by 20 cm subplots were laid out 1 m apart. The 5 squares with high density of *D. carota* are referred to below as the "north plots" and the 5 squares with high density of *G. crinita* as the "south plots." Fifty seeds from Radio Lab plants of both species were sown in each of the 20 subplots in November 1988.

Emergence and survival of marked seedlings were recorded on the following dates: 25-29 May, 11-13 July, 3-6 September, and 31 October - 2 November. Chewing damage was also estimated on these dates in the same 4 categories as in the transect study (i.e., < 10%, 10 to 49%, 50 to 74%, $\geq 75\%$). At the last census date the rosette diameters of 25 randomly selected plants of each species were measured in each subplot. If fewer than 25 plants were present then all were measured.

Plant cover was estimated by eye in July, using a grid of 25 four by four cm squares. Soil moisture was measured in the center of each plot on 18th August in the same way as for the transect. Soil samples were collected in November around the center of each plot. A volume equivalent to three 10 cm cores was taken from each plot with a 2 cm diameter soil corer. The samples were analyzed by Cornell's Nutrient Analysis Laboratories as described in Section I.

Results

Soil factors varied in much the same way as for the north and south ends of the transect. Soil moisture tension in August was slightly greater in the north zone, i.e. the soil was drier ($p = .046$, Mann-Whitney test on averages from each pair of subplots). Soil pH (dry samples; Mann-Whitney $p = .009$), magnesium ($p = .028$), calcium ($p = .009$), and manganese ($p = .009$) were all at higher levels in the south plots, while potassium ($p = .036$) and organic matter index (loss on ignition, $p = .03$) were higher in the north plots. Levels of phosphorus, iron, aluminum, and zinc were not different in the two areas ($p > .05$). Plant cover, which may indicate to some extent the relative degree of interspecific competition, was not different between north and south plots.

As found for the transect, in contrast to what would be predicted from the distribution of flowering plants, survival of first-year *G. crinita* from May to November was greater in the north plots, in the zone of low density of flowering *G. crinita* and high density of *D. carota* ($p = .02$, Mann-Whitney test, data from subplot averages; median percent survival: north 84.1, south 57.5). There was no significant difference in survival of first-year *D. carota* between north and south plots ($p > .05$) although the trend was similar to that seen for *G. crinita* (median percent survival: north 51.2, south 25.0). *G. crinita* had greater survival than *D. carota* in the north plots ($p < .05$) but there was no difference between the two species in the south plots.

There were second-year *G. crinita* plants present within the south plots and none in the north plots. It is possible that intraspecific competition from older plants affected seedlings here, but among the

subplots no correlation was detected between number of second-year plants present in May and seedling survival percents from May to November (Spearman rank correlation, $p > .05$).

With regard to survival in relation to density of seedlings rather than flowering plants, the survival of *G. crinita* was lower in the southern subplots, where more seedlings of the species emerged. The density of seedlings in May was greater in these plots compared to the north plots (Mann-Whitney $p < .05$) because sown seed was supplemented by "native" seed originating from flowering plants in the southern part of the field. Similarly there were more *D. carota* seedlings in the north plots compared to the south plots (Mann-Whitney $p < .05$) although survival was not different between the two areas.

G. crinita seedlings grew more, as measured by rosette diameter in November, in the north plots (Mann-Whitney $p = .009$). Median rosette diameter was 60 mm in the north plots and 21 mm in the south plots. Rosette diameters of *D. carota* seedlings were not significantly different in November in the north plots compared to the south plots (Mann-Whitney $p > .05$), although median rosette diameters were 41 mm in the north and 29 mm in the south plots.

Analysis of the association of amount of chewing damage and subsequent survival was not possible for *G. crinita* in the north plots as few plants died and few were heavily damaged (4% had > 50% damage in July), whereas 14% were heavily damaged in the south. A comparison of the survival to September of plants in south plots that in July had < 10% damage (35.7% survival) or > 50% damage (53.7% survival) showed that greater mortality was associated with greater damage ($\chi^2 = 6.52$, $p = .011$). However, even plants with < 10% damage had greater mortality in the south than north plots ($\chi^2 = 24.24$, $p = .0001$). Of course the greater mortality could still have been due to herbivory if seedlings in the south plots were totally eaten between census dates. So few plants died after September that analyses of differences between September and November were not possible.

Similar numbers of *D. carota* plants showed signs of chewing damage in both north and south plots. In July percents of plants with <10% damage were 50.8% in the south and 43.8% in the north, while percents of plants with >50% damage were 39.7% in the south and 34.1% in the north. *D. carota* showed no difference in mortality by September in relation to amount of chewing damage (<10% or >50%) in July (χ^2 test, $p > .05$). As with *G. crinita*, even plants with <10% damage in July had greater mortality between July and September in the south rather than the north plots ($\chi^2 = 25.79$, $p = .0001$).

Transplants of *G. crinita* in pots

In a further attempt to find out whether the distribution and abundance of *G. crinita* could be significantly limited by herbivory, a small transplant experiment was undertaken in 1989 in the Ithaca area.

Methods

Plants that had been grown in Cornell mix in the greenhouse were transplanted in their pots on 14th August to two sites: the Radio Lab field at the edge of the *G. crinita* population, and 6 km to the south near Turkey Hill (76° 26' N, 42° 26' W), at the edge of an old field where no *G. crinita* population existed. This site was where the "mildly acid" soil used for the soil type greenhouse experiment described in Section III was collected. *G. crinita* grew well in this soil in the greenhouse (see Section III). Grasses predominated at both sites, and average vegetation height was about 35 cm.

At each site two sets of four pots were placed in holes dug so the pot surface was level with the ground surface. Each set consisted of two pots of second-year *G. crinita* (16 in one pot, 25 in another; pots were 12 by 12 cm, 6 cm deep), and two pots of first-year plants (16 in one, 2 in another; pots were 8 by 8 cm, 6 cm deep). The pots were arranged at the corners of a 4 by 4 m square. The

second-year plants each had one flower bud. Pots were visited biweekly until 2nd November to observe herbivory and other damage.

Results

More damage by animals to first-year plants was noted at Turkey Hill than at the Radio Lab (Table 5.7), although similar numbers of second-year plants had flowers nipped off by deer or small mammals. Four of the 41 plants managed to reach seed dispersal stage at the Radio Lab, compared to one of 41 at Turkey Hill (Table 5.7).

Table 5.7. Comparison of herbivory damage to transplants of *G. crinita* at Turkey Hill and the Radio lab field, observed biweekly between 14th August and 2nd November 1989 (2 pots of first-year and 2 of second-year plants at each site). Second-year plants had one flower bud each. Herbivores may have included deer, small mammals, slugs (observed in the pots), and insects.

First-year seedlings:

<u>Initial number</u>	<u>Number observed that were bitten off at the base</u>	<u>Number remaining in November *</u>	<u>Chewing damage on the survivors</u>
<u>Turkey Hill</u>			
16	7	0	--
2	0	1 **	20% of foliage
<u>Radio Lab</u>			
16	0	5	± 15% of foliage of each
2	0	2	one < 5%, one ± 20%

Second-year plants:

<u>Initial number</u>	<u>Number with flowers nipped off</u>	<u>Number with mature seed capsules***</u>
<u>Turkey Hill</u>		
16	4	1
25	13	0
<u>Radio Lab</u>		
16	3	3
25	10	1

* Most other seedlings disappeared between censuses. They may have been chewed or bitten off, or may have died for other reasons.

** The other one was dug up, apparently by a small mammal.

*** Other plants disappeared between censuses, had shrivelled flowers, or the flowers had been nipped off.

Summary of Section II

Within the Radio Lab field, patchiness in the abundance of the existing population of *G. crinita* was positively associated with higher levels of certain soil factors. However, patterns of survival, growth, and reproductive output in 1989 were found to be negatively related to these factors. The abundance of *G. crinita* was greater where levels of soil moisture, pH, calcium, magnesium and manganese were higher, and where potassium, organic matter, and plant cover were lower. *D. carota* showed the opposite pattern of association. In contrast, survival of *G. crinita* seedlings was lower and rosettes were smaller in 1989 in parts of the field where abundance of the species was greater, and where soil moisture, pH, calcium, magnesium, and manganese were at higher levels and potassium and organic matter were at lower levels. Interspecific competition, represented by plant cover, and intraspecific competition from second-year plants, seemed to have little effect on survival and growth of *G. crinita* seedlings. These differences in survival would be likely to persist into the beginning of the following year at least, if the same pattern was followed as in 1988-89 when overwinter survival was related to rosette size attained during the first season's growth. However, second-year plants along the transect showed no differences in survival during the 1989 growing season.

Reproductive performance showed a similar pattern to that of survival and growth of first-year *G. crinita* plants. Reproductive output, represented by height of plants, was greater where levels of pH, calcium and manganese were lower and potassium and organic matter were higher, although no correlation was found with soil moisture, plant cover, or density of second-year plants.

D. carota seedlings survived better where first-year plants were less dense along the transect, but no difference in size was detected. No differences in survival and size of seedlings were seen when plots in the north part of the field, where seedlings were more abundant, were compared to plots in the south part of the field, where seedlings were less abundant. Like *G. crinita*, survival of *D. carota* plants more than one year old was not related to soil factors or plant cover along the transect.

The amount of damage caused by herbivores to first-year plants appeared to have relatively little effect on the survival of either species in the Radio Lab field. However the pot transplant experiment suggested that *G. crinita* might suffer more from herbivore damage in locations without *G. crinita* populations that would otherwise be favorable in terms of plant cover and soil type, than in sites with established populations.

SECTION III. GREENHOUSE EXPERIMENTS TO TEST THE EFFECT OF SOIL TYPE AND SOIL MOISTURE ON SEEDLING EMERGENCE, SURVIVAL, AND SIZE OF *G. crinita*

To test whether soil type and soil moisture were major causal factors affecting the distribution, abundance, survival, and performance of *G. crinita*, three greenhouse experiments were carried out in 1988-89. The rationale for the experiments was based on previous work.

Preliminary studies

Information from the literature (Chapter 2) and preliminary analyses of soil pH in 1987 and 1988 from a number of *G. crinita* localities using a Cornell pH test kit suggested that *G. crinita* was often associated with soil types which had a pH greater than 7. This finding was confirmed in the site survey of 1989 (Section I). A preliminary study in the greenhouse in 1988 also suggested that *G. crinita* performed better in soils with a high rather than low pH, while *D. carota* was less affected by pH at two levels of moisture. Markedly fewer plants of *G. crinita* established from seed sown in Cornell mix amended with aluminum sulphate to lower the pH to 5.0 than established in Cornell mix amended with dolomitic lime to raise pH to 7.2, measured using a Cornell pH test kit. *G. crinita* and *D. carota* were sown separately (50 seeds per pot, 12 pots per treatment) in the fall 1987, overwintered on a flat roof at Cornell University, and kept in the greenhouse from 12th May to 12th December 1988. One

half of the pots were placed in trays which drained freely through holes in the base of each tray. The other half were put in trays which retained water because drainage holes were located partway up the sides of each tray. Average establishment percents were:

<u>Pot type</u>	<u><i>G. crinita</i></u>		<u><i>D. carota</i></u>	
	<u>High pH</u>	<u>Low pH</u>	<u>High pH</u>	<u>Low pH</u>
Free drainage	19.3	3.5	35.4	29.2
Impeded drainage	23.9	3.8	37.3	20.2

To test whether, under more natural conditions, emergence and survival of *G. crinita* were more limited by soil type compared to *D. carota*, soils were collected from the field for a greenhouse experiment in 1988-89, which is described in detail below.

The impact of the drought in 1988, described in Section II, suggested that soil moisture has a key role in determining relative abundance and distribution of *G. crinita* and *D. carota* in the Radio Lab field. Two greenhouse experiments to test whether *G. crinita* was less favored by dry soils and more favored by wetter conditions than *D. carota* were carried out in 1988-89 and are described after the soil type experiment.

Greenhouse experiment with 3 soil types

Methods

In November 1988, seeds of the two species were collected from the Radio Lab field and sown separately in three different soils: (a) calcareous silty clay loam, pH 7.8, from a valley floor marsh (76° 51' N, 42° 21' W) (b) mildly acidic loam, pH 6.5, from the edge of an old field (76° 26' N, 42° 26' W) and (c) acidic loam, pH 4.8, from a roadside bank bordering an old field (76° 21' N, 42° 22' W). None of these sites had *G. crinita* populations. Soil was collected from the upper 10-15 cm of the profile, but loose litter was excluded. Soil pH was measured with a Cornell pH test kit at the time of collection. Large stones greater than 10 mm diameter and root fragments were removed from soils by sieving, and 60 pots 8 by 8 cm, 6 cm deep, were filled with each soil type. Each pot was sown with 25 seeds of *G. crinita* or *D. carota*, and then the pots were placed on a flat roof at Cornell University over the winter. On 15th March 1989, they were brought into the greenhouse.

Seedling emergence began on 24th March and was recorded every other day until 17th April. On 7th May the seedlings were thinned to one per pot, and survival and rosette diameter were recorded on 22nd August 1989. The plants were then harvested, including roots, which were extracted by carefully washing in water. The samples were dried in an oven at 41° C for several days and weighed.

Pots were in trays randomly arranged on the greenhouse bench. Pots were rearranged within trays and trays rearranged on the bench every 3 to 4 weeks. The soils were kept moist by regular watering with de-ionized water. After the end of the experiment, soil from a composite sample of three pots from each type was sent to Cornell's Nutrient Analysis Laboratories. Analysis was done in the same way as for the site survey soils (Section I) and texture was also analyzed as described in that section.

Results

The results of the soil analyses (Table 5.8) show that in comparison to the site survey (Table 5.1) the acid soil used in the greenhouse experiment had a lower pH, lower available calcium and higher aluminum than any of these soils. The other two soils had nutrient levels within the range found in the

site survey. The calcareous type had a higher silt and lower sand content than any of the site survey soils.

Seedling emergence of *G. crinita* did not differ between the three soil types (χ^2 test, pooling emergence data in each type). *D. carota* had lower emergence in the acid soil compared to the other 2 types ($\chi^2 = 28.07$, $p < .005$), even though overall percents in each type were higher than *G. crinita* (Table 5.9). All χ^2 comparisons between species were significant at $p = .0001$ ($\chi^2 = 34.65$, 137.48, 85.46 for emergence of the two species in acid, mildly acid, and calcareous soils, respectively). These results together with the similar findings in the preliminary 1988 experiment suggest that *D. carota* had overall higher emergence in a range of soils. However, it should be noted that *D. carota* emergence was not always greater than that of *G. crinita*. Percent emergence of *D. carota* in other experiments was found to be similar to *G. crinita* or lower (Fall 1989 soil moisture experiment in this section, below; and Chapter 3, Sections I and II).

Survival of *G. crinita* was much lower in the acid soil but survival percents of *D. carota* were very similar in all three soils (95% binomial confidence intervals, constructed as in Blyth & Still 1983, were overlapping). Inspection of binomial confidence intervals suggests that the two species survived equally well in the calcareous and mildly acid soils but that *G. crinita* had lower survival than *D. carota* in the acid soil (Table 5.9).

G. crinita grew larger in the mildly acid soil than in the acid or calcareous soils, as did *D. carota*, but neither species differed in rosette diameter when acid and calcareous soils were compared (Table 5.9). Rosette diameter in *G. crinita* was strongly correlated with biomass, represented by dry weight ($\rho = 0.928$, Spearman rank correlation, $p < .00001$), and significantly correlated in *D. carota* though less strongly ($\rho = 0.475$, $p < .0001$). However, when biomass of plants from the different soil types was compared, while plants from the mildly acid soils were again the largest, plants from the calcareous soil also had significantly greater biomass than plants grown in the acid soil (Table 5.9). Biomass included weight of roots as well as shoots. Roots were poorly developed in *G. crinita* and *D. carota* plants from the acid soil, as examination of the shoot:root ratios showed (Table 5.9).

Table 5.8. Analysis of three soils used in the greenhouse experiment to study seedling emergence and survival of *G. crinita* and *D. carota* in different soil types.

	Acid soil	Mildly acid soil	Calcareous soil
pH (dry soil)	4.7	6.2	7.6
Organic matter (% loss on ignition)	8.7	9.4	11.5
Phosphorus (ppm)	0.7	1.7	9.7
Potassium	57	134	62
Magnesium	39	230	496
Calcium	239	2193	13373
Iron	13	3	16
Aluminum	238	20	15
Manganese	15	35	87
Zinc	4.1	0.8	2.8
Clay* (% by volume)	17.7	22.6	36.9
Silt	43.0	43.0	63.0
Sand	39.3	34.4	0.1
* USDA system: < .002 mm = clay, .002 to .05 mm = silt, .05 to 2 mm = sand.			

Table 5.9. Seedling emergence, survival percents, and size of *G. crinita* and *D. carota* in three soil types in the greenhouse. Emergence data for each species are pooled from 750 seeds (25 per pot, 30 pots) sown in each soil type. Survival percents are of 30 plants of each species in each soil type, with 95% confidence intervals (calculated as in Blyth & Still 1983). Plant sizes are of those individuals surviving to harvest in each treatment. Values with the same superscript letter indicate that mean ranks were not significantly different among soil types at $\alpha = .05$ (within species), using multiple comparison tests (as in Conover 1980).

SOIL TYPE									
ACID			MILDLY ACID			CALCAREOUS			
<u>Seedling emergence (%)</u>									χ^2 <u>p value</u>
<i>G. crinita</i>	35.9		33.7		37.3		2.14		.34
<i>D. carota</i>	50.9		64.0		61.2		29.29		.0001
Acid			Mildly acid			Calcareous			
<u>Survival</u>	<u>n</u>	<u>%</u>	<u>C.I.</u>	<u>n</u>	<u>%</u>	<u>C.I.</u>	<u>n</u>	<u>%</u>	<u>C.I.</u>
<i>G. crinita</i>	4	13.3	(5-30)	29	96.7	(84-100)	25	83.3	(65-93)
<i>D. carota</i>	29	96.7	(84-100)	29	96.7	(84-100)	30	100	(89-100)
<u>Median rosette diameter (mm)</u>							Kruskal-Wallis		
							H	<u>p value</u>	
<i>G. crinita</i>	8	^a		35	^b		10	^a	
<i>D. carota</i>	275	^a		326	^b		272	^a	
<u>Median total biomass (mg)</u>							Kruskal-Wallis		
							H	<u>p value</u>	
<i>G. crinita</i>	1.1	^a		60.3	^c		4.3	^b	
<i>D. carota</i>	400	^a		800	^c		635	^b	
<u>Median shoot:root ratio</u>							Kruskal-Wallis		
							H	<u>p value</u>	
<i>G. crinita</i>	6.61	^a		1.73	^b		1.25	^c	
<i>D. carota</i>	0.62	^a		0.52	^b		0.53	^b	

Greenhouse experiment with 5 moisture treatments

Methods

The response of *G. crinita* and *D. carota* to a range of moisture conditions was tested in an experiment set up in the autumn of 1988. Seeds from the Radio Lab field were collected in the fall and 25 seeds of each species were sown separately, either in Cornell mix amended with dolomitic lime so pH reached 7.2, or in calcareous soil collected from the same valley marsh location as the soil used in the soil type experiment described above (pH 7.8). This calcareous soil more closely resembled most soil texture conditions found in *G. crinita* localities compared to the highly organic Cornell mix. Each species was sown in a total of 90 plastic pots, 7 cm diameter at the base, 10 cm deep, filled to 7-8 cm depth with Cornell mix or soil (45 pots of each substrate). The pots were overwintered on a flat roof at Cornell University and brought into the greenhouse on 15th March 1989. Germination began on 25th March and plants were allowed to establish for about 4 weeks before being thinned to the one seedling nearest the center of each pot, on 28th April. The pots were sprayed with water regularly and as evenly as possible.

On 6th May pots were assigned to five moisture treatments, with 9 pots of each species and substrate allocated to each treatment. To try to reduce an initial source of variation between treatments due to different moisture contents and soil quantities at the start of the experiment, a restricted randomization scheme was adopted. For each species the 45 pots in each substrate type were ranked by pot weight and divided into 9 groups of 5 pots. Within each group treatments were randomly assigned to pots so that each treatment was represented over the whole range of pot weights. Pots were arranged in a completely randomized design on the greenhouse bench. The treatments were:

1. 'Very dry': Pots were watered from above with 25 ml per pot.
2. 'Dry': Pots were watered from above with 40 ml per pot.
3. 'Moist': Pots were placed in 10 cm dia. containers, 4.5 cm deep, with 4 holes drilled at 1 cm from the base. Water was poured into the outside container until it overflowed out of the holes.
4. 'Wet': Pots were placed in containers as in treatment 3, but the holes were drilled 3 cm from the base so that a greater quantity of water was held by the outer container.
5. 'Waterlogged': Pots were placed in 12 by 12 cm pots, 6 cm deep, lined with plastic. The outer pot was filled with water so that the water level was within 1-2 cm of the substrate surface.

The frequency of watering was based on readings from a set of unseeded pots of both substrates, subjected to the 5 treatments, which contained ceramic blocks attached to electrodes. Soil moisture percent, measured by the electrical resistance in the blocks, was recorded with a meter (Model 5910A, Soilmoisture Equipment Corp.) and each value adjusted relative to the meter reading for blocks when they were saturated, which was less than 100% in all cases. Pots were watered when meter readings in the dry soil treatment fell below 10% (unadjusted). The typical pattern of soil moisture changes under the regimes is shown in Fig. 5.14. When 'dry' reached 10%, 'very dry' usually had fallen below 5%, no water remained in the containers of 'moist' pots, and < 1 cm of water in containers of 'wet' pots. The Cornell mix never became as dry as the soil and had a much greater water holding capacity (Fig. 5.14). For instance the moisture reading in the dry treatment never fell to 10%. When saturated, a weighed sample of Cornell mix held 722% of the dry weight of the same sample, whereas the soil when saturated held only 94% water by weight.

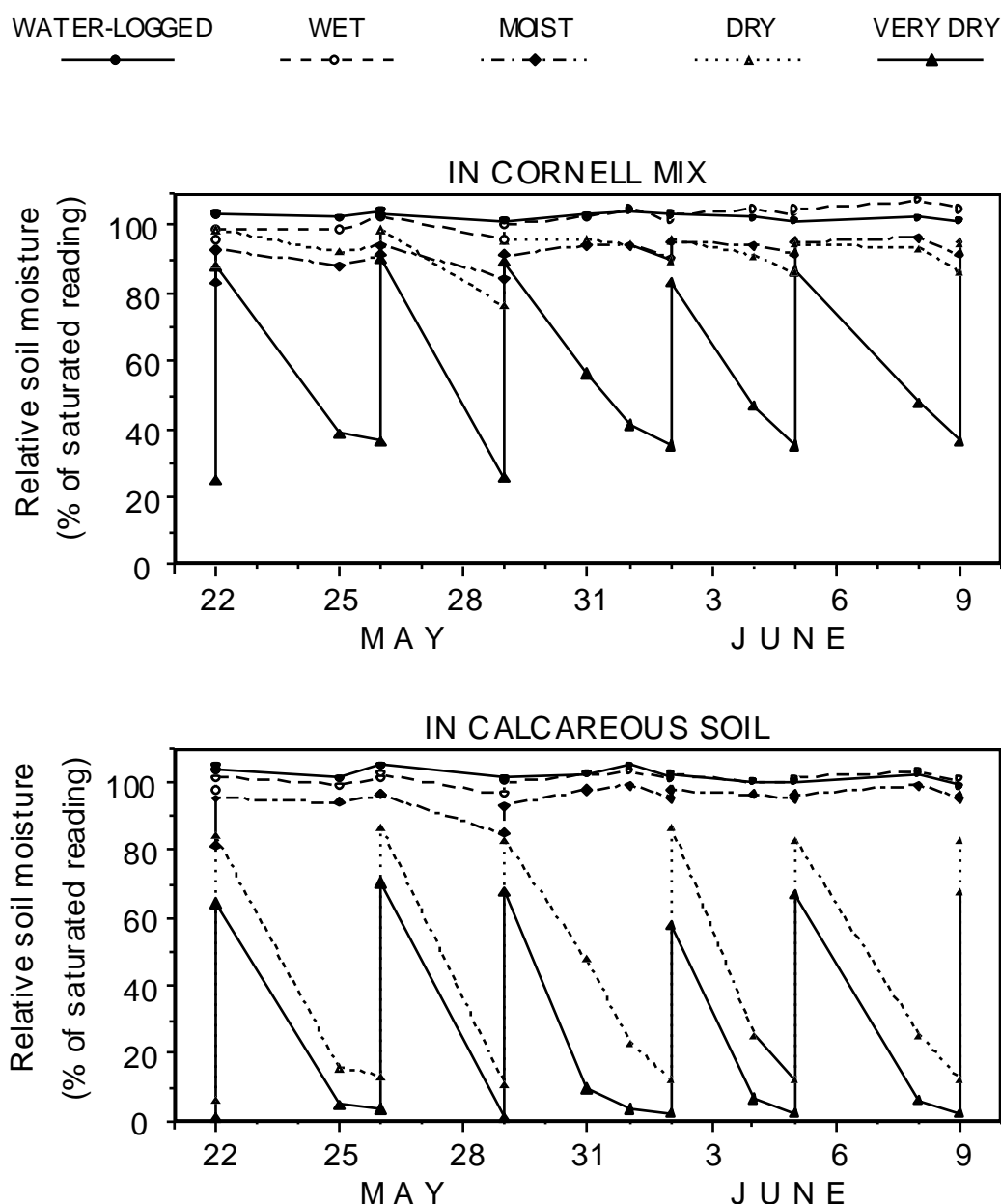


Fig. 5.14. Pattern of changes in soil moisture in pots of Cornell mix and calcareous soil with 5 moisture treatments over a representative period. Pots were watered when the moisture meter reading in the pot of calcareous soil in the dry treatment fell below 10 units ($< 14\%$ moisture). Soil moisture was measured with gypsum blocks buried halfway down the substrate depth in each pot. Meter readings were adjusted to percent of the value at saturation for each block at the beginning of the experiment, which in some cases was less than subsequent meter readings.

The watering regime did change pot weights considerably, suggesting that initial differences in the quantity of substrate and soil moisture content were overridden. By 26th May, weights of pots with Cornell mix and *G. crinita* (which had negligible weight) were significantly different among the 5 treatments ($p = .0001$, overall F test, Proc GLM ANOVA, Scheffé test of means, $\alpha = .05$). The soil treatments also were significantly different in weight ($p = .0001$) although dry and very dry treatments were not different, nor were wet and waterlogged (at $\alpha = .05$, Scheffé test), probably because water formed a smaller proportion of the weight of each pot and differences in amount of soil were more

important. Because of the strong treatment effect on pot weight, the statistical "blocking" factor of initial weight was therefore ignored in the subsequent analysis.

Rosette diameters of the plants were measured every few weeks. The data for 27th July are reported for *G. crinita* as after that date some plants were killed when the pots were treated on August 4th with an insecticide drench to control fungus gnat larvae. The larvae were abundant in the wet and waterlogged pots and could have damaged roots (K. Goodwin, Cornell, pers. comm.). Granules of diazanone in an oil base were used, and some plants were killed within 24 hours. Other *G. crinita* and all *D. carota* appeared to be unaffected. The pots had been treated on 2nd June with diazanone in the form of a water soluble powder apparently without affecting any plants. All mortality in the Cornell mix pots had happened before 2nd June. Four plants in the soil died before 2nd June and 10 died between 2nd June and 27th July, mainly in wet and waterlogged pots, but the remaining plants grew as much as or more than plants in other treatments (see below) so it was considered reasonable to use the size data collected on 27th July. Recording of *D. carota* was continued until 24th August when the plants were harvested, dried at 41°C for several days, then weighed.

Results

The rosette diameter of *G. crinita* grown in Cornell mix differed between watering treatments on July 27th (Kruskal-Wallis test, $H = 13.13$, $.01 < p < .025$). Multiple comparisons among mean ranks (as in Conover 1980) revealed that plants in dry and very dry treatments grew less than plants in the moist and wet treatments, though plants in the dry treatment were not different in size from those in the waterlogged treatment (Fig. 5.15). No significant differences in rosette diameter between watering treatments were detected in the plants grown in the soil pots ($H = 8.48$, $p > .05$; critical value at $\alpha = .05$ is 9.49) although there was a similar trend in the data. Fig. 5.15 shows that the plants in the dry treatments again tended to be smaller.

Rosette diameters of *D. carota* were significantly different in July in both Cornell mix ($H = 15.7$, $p < .005$) and in soil ($H = 19.22$, $p < .005$). Multiple comparisons of mean ranks detected some differences (Fig. 5.16); generally plants in the moist treatment had the largest rosettes while plants in the dryer treatments were smaller than those in the wetter treatments.

However, biomass showed the opposite pattern. Biomass of *D. carota* in August showed clear differences among watering treatments, in both substrates (Cornell mix, $H = 20.51$, $p < .005$; soil, $H = 37.46$, $p < .005$). Plants in the very dry, dry, or moist treatments in Cornell mix and in soil all had greater biomass than plants in wet or waterlogged treatments, and in soil, plants in the moist treatment had the greatest biomass, and plants in very dry and dry treatments had greater biomass than plants in wet or waterlogged treatments (Multiple comparisons, $p < .05$; Fig. 5.16).

The evidence for the relatively better performance of *G. crinita* in wetter soils, and the converse for *D. carota*, in terms of biomass at least, is supported by a comparison of their performance in the two substrates. Overall, *G. crinita* plants grown in the soil were smaller than plants grown in Cornell mix, while *D. carota* plants grew larger in the soil than in the Cornell mix (Mann-Whitney tests, $p < .0001$ for each species). As explained in the methods, Cornell mix has much greater water holding capacity. It seems unlikely that differences in nutrient levels could explain the performance differences, as the species responded in opposite ways.

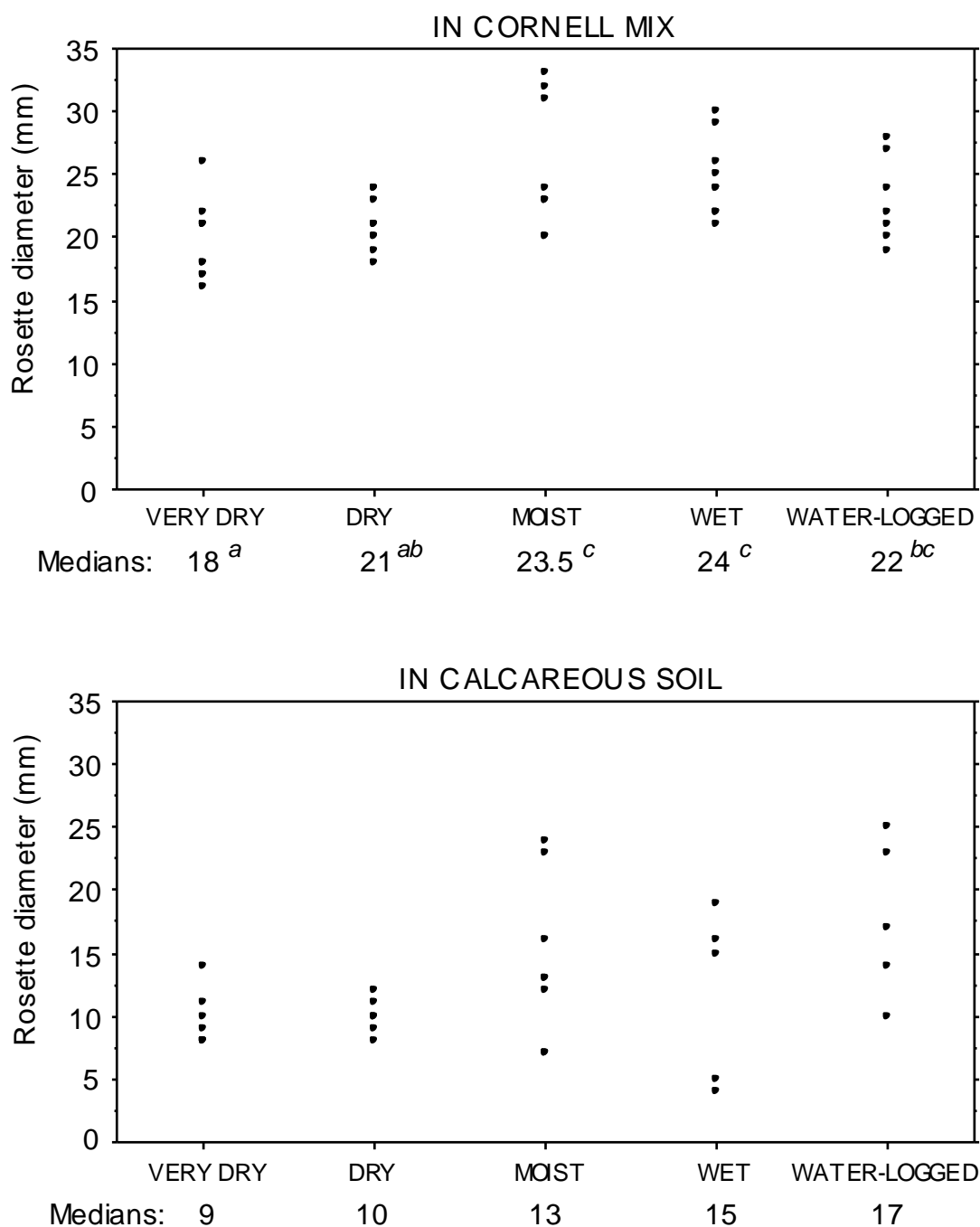


Fig. 5.15. Comparison of *G. crinita* rosette diameters ($n = 5$ to 9) after 4 months in the 1988-89 greenhouse experiment, with five moisture treatments and two substrates, Cornell mix or calcareous soil. In Cornell mix, treatments with the same letter (a, b, c) were not significantly different at $\alpha = .05$, using multiple comparisons among mean ranks from Kruskal-Wallis tests. The Kruskal-Wallis test for sizes in calcareous soil was not significant, but there was a similar trend to smaller plants in drier conditions.

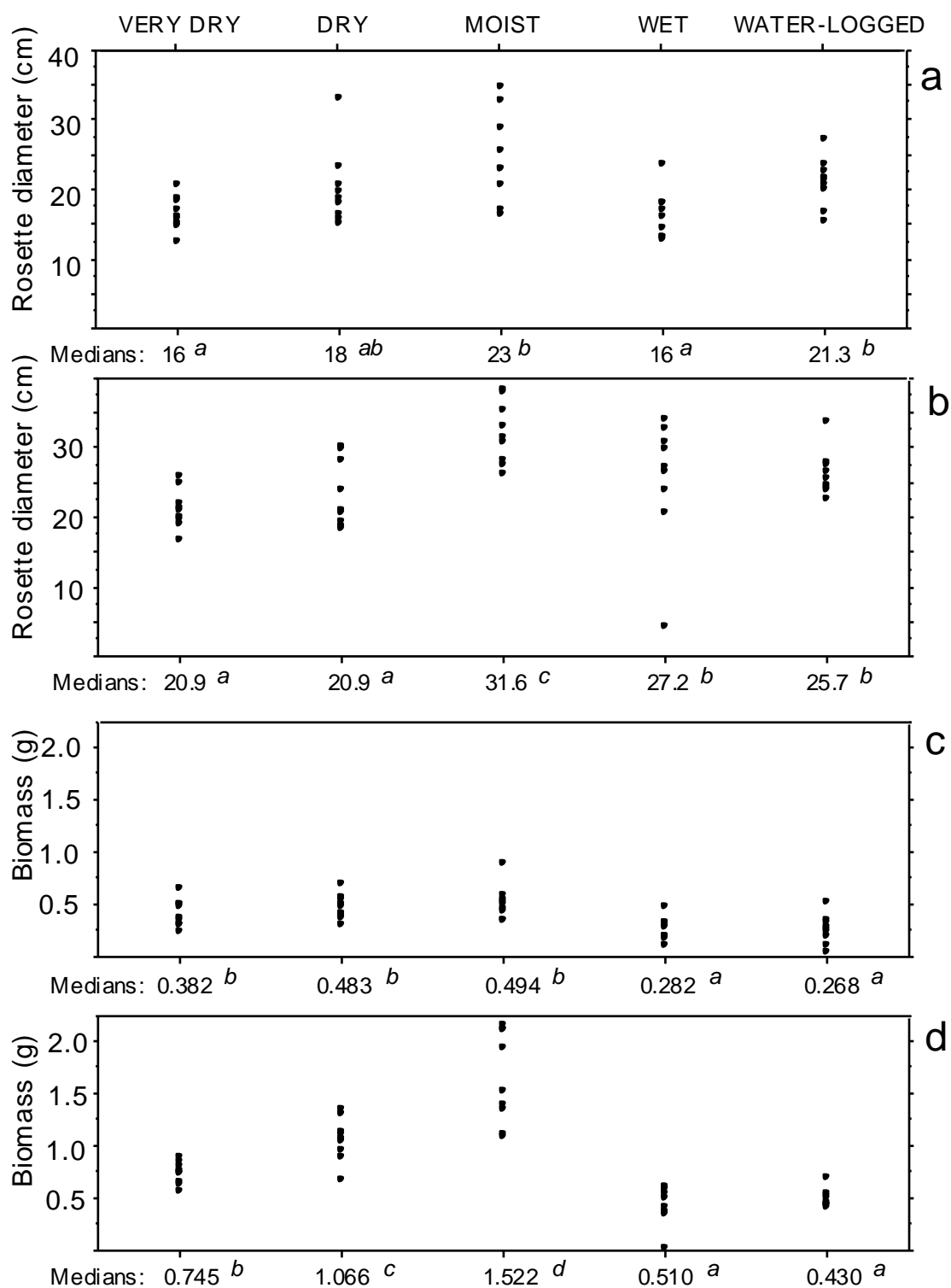


Fig. 5.16. Comparison of *D. carota* sizes in the 1988-89 greenhouse experiment, with 5 moisture treatments and 2 substrates: rosette diameter July 27 in a) Cornell mix or b) calcareous soil; and biomass in August (5 months' growth) in c) Cornell mix or d) calcareous soil. Medians with the same letter were not significantly different, using multiple comparisons of mean ranks.

Greenhouse experiment: moist vs. waterlogged conditions

The preceding experiment did not follow the response of plants to different moisture conditions during seedling emergence and during the earliest stages of seedling growth. To investigate the relative performance of the two species over that period and to confirm the pattern apparent in this experiment without any interference from possible pesticide side effects, a follow-up experiment was set up in the greenhouse in the fall of 1989.

Methods

The experiment was set up using seed of *G. crinita* and *D. carota* collected one year before and stored dry in a refrigerator, then stratified for 4 weeks by being floated on distilled water in petri dishes, again in the refrigerator. Seed was sown on 22nd November, separately, 50 seeds per pot, in 20 pots assigned to two moisture treatments. Pots were 10 cm dia. and 10 cm deep, filled with 6 cm of Cornell mix. In the moist treatment, pots were regularly sprayed with water but were freely drained. Pots in the other treatment were placed in outer pots (12 by 12 cm, 6 cm deep) lined with plastic and filled with water so the Cornell mix was completely waterlogged. The outer containers were refilled whenever levels dropped 1 cm below the surface of the substrate, and pots were sprayed at the same times as the freely drained pots. Pots were randomly arranged on the greenhouse bench and the plants were grown without supplemental lighting.

Seedling emergence began on 30th November and was recorded until 28th December. Plants were thinned to 5 per pot on 7th December, and to 1 per pot (the one nearest to the center of each pot) on 14th December. Subsequently any new seedlings were recorded and then removed every 2-3 days. On 28th December plants were measured and harvested. Samples were dried in an oven at 41°C for several days and weighed.

Results

For both species, more seedlings emerged in the moist pots than in waterlogged pots (χ^2 tests of total emergence, from 500 seeds sown in each treatment).

	<u>Percent emergence</u>		χ^2	p
	Moist	Waterlogged		
<i>G. crinita</i>	89.6	54.2	155.1	.0001
<i>D. carota</i>	39.8	21.4	39.9	.0001

The lower percent emergence of *D. carota* compared to *G. crinita* may have been due to the relatively wet conditions of both treatments, or storage may have reduced viability of the *D. carota* seed to a greater extent.

There was no mortality during the experiment; both species were able to survive several weeks of waterlogged conditions. However, *D. carota* grew less in the waterlogged pots than in moist pots (Mann-Whitney test of rosette diameter, $p = .002$; median diameter 36 mm vs. 103 mm). Biomass was also significantly less in waterlogged pots ($p = .003$; median dry mass 1.7 mg vs. 7.23 mg in moist pots). In contrast *G. crinita* showed no differences in rosette diameter or biomass between moist and waterlogged treatments ($p > .05$); median rosette diameters were 8.5 and 7.5 mm, median biomass 0.174 and 0.135 mg, respectively.

Summary of Section III

G. crinita had much lower survival and grew less in an acid soil type compared to mildly acid or calcareous soil types, although seedling emergence was similar in all three types. Seedlings grew

largest in mildly acid soil. Seedling emergence of *D. carota* was lowest in acid soil but survival was similar in the three soil types. As found for *G. crinita*, plants grew least well in the acid soil and best in the mildly acid soil.

Seedlings of *G. crinita* tended to grow larger in moist or wet substrates compared to dry substrates. For at least the first few weeks after emergence, seedlings could grow equally well in moist or waterlogged substrates, although emergence was lower in waterlogged conditions. Biomass of *D. carota* plants was lower in wetter substrates compared to dry or moist conditions, and seedling emergence was lower in waterlogged substrates compared to moist substrates.

DISCUSSION

The results described in the three preceding sections present a rather complex picture for interpretation. To assist in clarifying how the results relate to each other, a summary is set out in Table 5.10. It gives the responses of the two species, measured by particular life history characteristics such as survival of first-year plants and reproductive output, that were recorded in the various experiments and observational surveys. It provides the basis for the following discussion of (a) the factors limiting populations of *G. crinita* and of (b) the wider ecological relevance of the findings in terms of habitat specialization, physiological versus ecological performance optima, and population "refuges."

Table 5.10. Summary of the results of the site survey in New York State, within-site studies at the Radio Lab field, and greenhouse experiments. (*Gentianopsis crinita* (Gc): plain type; *Daucus carota* (Dc): in italics).

Experiment or observation	LIFE HISTORY CHARACTERISTICS
	<u>Distribution</u>
Survey of 32 sites in New York	Gc: Mostly on neutral-alkaline soils, good moisture supply. Sites unwooded, usually in short herbaceous vegetation.
Radio Lab, 30 m transect north to south	Gc: Found in south part of field where pH, Ca, and soil moisture higher. Dc: <i>Found all along transect.</i>
	<u>Abundance</u>
Survey of 32 sites in New York	Gc: Density not related to soil factors or plant cover.
Radio Lab, 30 m transect north to south	Gc: More abundant in south, where pH, Ca, Mg, Mn, soil moisture higher; K, organic matter, and plant cover lower. Dc: <i>Less abundant in south, where pH, Ca, Mg, Mn, and soil moisture higher; K, organic matter, and plant cover lower.</i>
Radio Lab, seed transplants into north and south plots	Gc: Density (native & transplants) greater in south, where pH, Ca, Mg, Mn, soil moisture higher; K, organic matter lower. Dc: <i>Density greater in north where pH, Ca, Mg, Mn, soil moisture lower; K and organic matter higher.</i>
Greenhouse soil type expt.: acid/mildly acid/calcareous soil	Gc: No difference in initial abundance (i.e. seedling emergence) between soil types. Dc: <i>Emergence lower in acid soil.</i>
Soil moisture expt.: moist & waterlogged	Gc: Initial abundance (seedling emergence) lower in waterlogged substrate. Dc: <i>Emergence lower in waterlogged substrate.</i>
	<u>Survival</u>
Radio Lab, 30 m transect south	Gc: Greater where density (abundance) lower, for 1st year seedlings. No relation between survival of north to 2nd year plants and soil factors or plant cover. Dc: <i>Greater where density lower, for 1st year seedlings. No relation between survival of 2nd year plants and soil factors or plant cover.</i>

Table 5.10 (continued)

	<u>Survival (continued)</u>
Radio Lab, seed transplants into north and south plots	Gc: Greater survival of 1st year plants in north plots, where pH, Ca, Mg, Mn, soil moisture lower; K, organic matter higher -- and where abundance of <i>D. carota</i> higher. Dc: <i>No difference between north and south.</i>
Transplants in pots, to sites with/without <i>G. crinita</i>	Gc: Greater survival of 1st year plants in existing <i>G. crinita</i> site.
Greenhouse soil type expt.	Gc: Much lower in acid soil. Dc: <i>No difference in survival among soil types.</i>
Soil moisture expt.: moist & waterlogged	Gc: No difference. Dc: <i>No difference.</i>
	<u>Growth in first year</u>
Radio Lab, 30 m transect north to south	Gc: Greater where density lower. Dc: <i>No relation to density.</i>
Radio Lab, seed transplants into north and south plots	Gc: Greater in north plots, where pH, Ca, Mg, Mn, and soil moisture lower; K and organic matter higher. Dc: <i>No difference between north and south.</i>
Greenhouse soil type expt.	Gc: Largest in mildly acid soil, smallest in acid soil. Dc: <i>Largest in mildly acid soil, smallest in acid soil.</i>
Soil moisture expt.: dry to waterlogged	Gc: Larger in moist and waterlogged than in drier substrates. Dc: <i>Smaller in waterlogged substrates than in moist and drier substrates.</i>
Soil moisture expt.: moist & waterlogged	Gc: No difference. Dc: <i>Larger in moist substrate than in waterlogged substrate.</i>
	<u>Reproductive output</u>
Survey of 32 sites in New York	Gc: Greater where pH and Ca lower and possibly where moderate amounts of soil moisture. Taller and may have more flowers where tall herb cover greater.
Radio Lab, 30 m transect north to south	Gc: Greater where pH and Ca lower, K and organic matter higher. No relation to amount of plant cover.
Transplants in pots, to sites with/without <i>G. crinita</i>	Gc: Greater in existing <i>G. crinita</i> site.

Factors limiting populations of *Gentianopsis crinita*

Edaphic factors

The hypothesis that *G. crinita*'s survival, growth, and reproductive output in unwooded landscapes are limited by a narrow range of soil conditions provided the focus for the investigations summarized in Table 5.10. The results of the site survey and transect study in the Radio Lab field indicated that the distribution of *G. crinita* is generally confined to neutral to alkaline soils with a plentiful supply of moisture. This finding accords with published information (see Chapter 2) and with comments made by staff of State Heritage Programs (Appendix I). Both sources frequently refer to *G. crinita* localities as having moist conditions (75% of all states in which it occurs) and calcareous substrates (50% of all states). There were only two instances of clearly contrary records. New Hampshire sites were noted as "dry" (Frankie Brackley, Heritage Program) and in eastern Pennsylvania localities were specified as acid to calcareous wetlands (Tom Smith, Heritage Program).

Statewide information also referred to the occurrence of *G. crinita* on soils developed on unusual igneous or metamorphic rocks such as serpentine, in four states towards the southern edge of its range in North America: Georgia, North Carolina, Maryland and Pennsylvania (Heritage Programs, and Reed 1986). In the first 3 states *G. crinita* populations may be restricted to soils developed from these rock types (Heritage Programs). A principal characteristic of serpentine soils is the greater levels of magnesium compared to calcium (Birse 1982). Soils at most *G. crinita* localities in New York State (27 of 32) had high or very high levels of magnesium (classification from Cornell Cooperative Extension 1990) although calcium always exceeded magnesium. It is not known if magnesium levels become critical in some way for *G. crinita* plants at the southern edge of their range. The association of range edge and serpentine is not unique to *G. crinita*. Dr. Alan Baker (Sheffield University, U.K.; pers. comm.) reports that there are other examples of species being found on serpentine or related rock types at their range edges.

The information on *G. crinita*'s distribution statewide, the distribution data from the site survey and Radio Lab, and the abundance data from the Radio Lab, seem to indicate that *G. crinita* favors alkaline, calcareous soil types. However the results on survival, growth, and reproductive output from all the relevant experiments and observations contradict this pattern by showing that *G. crinita* responds better to less calcareous and alkaline conditions, although the Radio Lab data are confounded by density differences. In fact the pH of some alkaline soils from the site survey may actually be lower than the soil analyses would suggest. As discussed in Section I, waterlogging may somewhat reduce the pH of alkaline soils nearer to pH 7 (Etherington 1982) so that pH in wet sites may sometimes be lower than that recorded during the soil analyses, which were done on dry soil. However, despite this qualification, the greenhouse experiment suggests that *G. crinita* can perform best on soils that are close to neutral but not alkaline, i.e. have a pH lower than 7.

The poor survival and growth of *G. crinita* plants in acid soil in the greenhouse would seem to explain their absence from these soil types in the field. The physiological cause may be related to aluminum toxicity. Levels were much higher in the greenhouse acid soil than any of the soils from the site survey (Tables 5.1, 5.8). The lack of root development in acid soil, which was particularly noticeable in *G. crinita* but also occurred in *D. carota* plants, was similar to what Rorison (1960a, b) found for *Scabiosa colombaria* grown in acid soil. *S. colombaria* is generally found on calcareous soils in England, and Rorison established experimentally that aluminum toxicity was the cause of its poor performance on acid soil.

In the field, *D. carota* was found in all except 4 of the *G. crinita* localities and had been present previously at 2 of these 4 (G. Chase, pers. comm.). In the greenhouse it demonstrated an ability to survive even on the acid soil, suggesting that its tolerance of soil type is wider than that of *G. crinita*. Interestingly, fewer *D. carota* seedlings emerged on the acid soil, where they grew least well,

compared to the other soil types, while no differences were seen in emergence of *G. crinita*. A similar pattern was found in the unfavorable scrub habitat in the Natural Area (Chapter 3, Section I). It may be that *G. crinita* responds to less precise germination cues than *D. carota*, resulting in high levels of seedling emergence in situations that are unfavorable for subsequent survival. Further investigation of germination requirements of these species and other common and rare species might be a fruitful avenue to explore in the search for ecological causes of plant species rarity.

Although *G. crinita* may survive across a range of soil types from mildly acid to calcareous, soil moisture appears to be the overriding factor limiting distribution. If locations with more favorable soil type have inadequate moisture in some years, as in the northern part of the Radio Lab field in 1988, *G. crinita*'s distribution will be confined to wetter areas, which may, by chance, have a soil type less favorable to growth and reproduction (e.g. a more calcareous and infertile soil). These combinations of soil moisture and soil type appear to have been responsible for the contradictory responses, in terms of distribution, abundance, survival, and reproductive output, which were recorded at the Radio Lab field. The co-occurrence of open ground, wetness, and alkalinity in *G. crinita* habitats is discussed further in the competition section below.

According to the site survey, populations of *G. crinita* may occur at lower elevations on cooler and damper north and east-facing slopes. This pattern of distribution may be because soil moisture is still sufficient at these elevations on north and east slopes, while it is insufficient on south and west facing slopes at the same elevations, as they receive greater insolation and thus have higher evaporation rates. However, the entire range of elevation among the sites in the survey was only 500 m, and it is surprising that such a difference in microclimate could result from relatively small differences in elevation between sites.

With regard to *G. crinita*'s moisture tolerance in soils that range from moist to waterlogged, the greenhouse experiments showed it could grow and survive as well in waterlogged compared to moist conditions although seedling emergence was lower. The site survey data, transplant results, and published information (Chapter 2) provided hints that growth or reproductive performance might sometimes be better on moist rather than wet soils, though the transect data from the Radio Lab showed no relationship between reproductive performance and soil moisture.

The abundance of *D. carota* in the drier northern part of the Radio Lab field, its widespread survival during the drought year of 1988, and its greater reproductive output in this year compared to 1987 and 1989 (Chapter 4), parallel the findings of the soil moisture experiments in the greenhouse. Here *D. carota* grew better in dry and moist rather than waterlogged substrates, though it did survive at these high moisture levels. The resilience to drought of the rosette "bank," i.e. plants more than 1 year old, compared to seedlings, as shown in 1988, has been noted in other facultative biennials (Klemow & Raynal 1985, de Jong & Klinkhamer 1988). Differences in root morphology may help to explain the tolerance of *D. carota* compared to *G. crinita*. *D. carota* can develop a mass of fine roots by the end of the first year's growth while *G. crinita* has rather few, sparsely branched roots (Chapter 2) and may be less efficient at exploiting soil moisture either in the first or second year.

Overall, although the distribution of *G. crinita* and *D. carota* overlaps, and *G. crinita* can sometimes grow well in areas with abundant *D. carota*, the evidence supports the hypothesis that *G. crinita* is limited by a narrower range of edaphic factors than *D. carota*, particularly with regard to soil moisture, and its narrower tolerance could help to explain its relative scarcity in the landscape.

The applicability of my results from *G. crinita* localities in New York State to other places across the range of the species may depend on how much genetic variation is present within the species. In particular the occurrence of ecotypes needs investigating, e.g. plants recorded from dry sites in New Hampshire and serpentine areas may represent different ecotypes. Information on genetic variation would also be of value to conservationists who may want to preserve as much genetic variation as

possible. In the absence of such information, the safest conservation strategy would seem to be to protect populations across the full geographic range of the species. Populations growing in a variety of edaphic conditions should also be conserved as part of a genetic conservation strategy.

Competition

The site survey confirmed the findings of Chapter 3, i.e. that *G. crinita* requires unforested conditions. Plants were sometimes observed growing close to scrub edges or at the borders of open woodland that had few shrubs in the understory. If this is a general feature throughout *G. crinita*'s range, it might explain the occasional published references to "thickets" and woods as habitats (e.g. Gleason 1952, Scoggan 1957). Alternatively there may be more shade-tolerant ecotypes in some localities.

Large expanses of bare ground were not a common feature of *G. crinita* localities in New York State, which accords with the results of experiments described in Chapter 3. In these experiments it was found that *G. crinita* could survive even in closed herbaceous vegetation as well as in relatively limited patches of bare ground. However, in closed swards in the Natural Area, survival and reproductive output were greater where competition from other species was reduced by clipping them. The negative association of numbers of plants and amount of plant cover along the Radio Lab transect might indicate that interspecific competition from herbaceous plants also affected *G. crinita*'s abundance in this site. However there was no relationship between reproductive output and plant cover along the transect, while first-year rosettes in the transplant plots grew larger in the northern part of the field even though plant cover was not different between north and south plots. The site survey also suggested that plants could grow taller and have more flowers where cover of tall herb vegetation was greater. It may be that such areas have soils with a higher nutrient status that overrides any deleterious effect of increased competition, which could explain the apparent contradiction to the results of Chapter 3.

Higher nutrient status may, however, facilitate colonization by shrubs and trees. It may be that *G. crinita* localities are often associated with past or present ground disturbance largely because of the impact of disturbance on colonization by woody plants. Severe disturbance in the past, resulting in loss of surface soil horizons and exposure of infertile subsoil as at the Radio Lab, may slow colonization by woody species while continual, current disturbance, for instance as at the Letchworth landslip, prevents anything more than patchy development of scrub or woodland. Of course *G. crinita* itself requires temporary stability. Individuals can be lost due to events such as gully erosion and deposition of material as seen at Letchworth, but as long as losses are localized, the population will persist.

The incidence of disturbance at *G. crinita* localities may be related to two other features, namely a plentiful water supply and calcareous substrates. The co-occurrence of these features in the landscape maybe more than a matter of chance. In the natural landscape the association of more or less permanently open, unstable ground with springs and saturated, mobile soil, as at Letchworth, provides an ideal habitat for *G. crinita*. Severe ground disturbance by humans, for example, due to extraction of low-lying deposits of marl, sand, and gravel, has resulted in other favorable moist habitats, e.g. the 3 marl marsh sites in New York State. As explained already, the calcareous conditions that are frequently associated with disturbance may not be particularly required by the plant. They may be a secondary feature of *G. crinita* localities, resulting from disturbance exposing unleached subsoil relatively high in bases such as calcium. However Boyer and Wheeler (1989) suggest that high levels of calcium inhibit productivity of fen vegetation by immobilizing phosphorus, and it may be that such infertile conditions play a role in keeping *G. crinita* sites open and unwooded for a considerable time. Thus while *G. crinita* may not perform best in calcareous soils, other plants -- particularly woody species -- may exhibit much poorer survival and growth in these soils than in more fertile, less alkaline soils.

Interspecific competition from herbaceous plants may have some influence on the distribution of *G. crinita* in waterlogged areas. The greenhouse experiments indicated that *G. crinita* can survive waterlogged conditions, but the site survey suggested that *G. crinita* cannot extend into very wet stands of cattail (*Typha* species). It may be that *Typha* and possibly other robust marsh plants exclude *G. crinita* from such waterlogged habitats by the production of high quantities of persistent litter. Bohlen (1990) found that removal of *Typha* litter could increase the number of associated herb species in cattail marshes in central New York. Presumably such large amounts of litter could similarly inhibit survival of *G. crinita*.

Intraspecific competition, as represented by various density-dependent effects, for example on survival and fruit output, has been found to limit abundance in several short-lived plants (Grubb et al. 1982, Grubb 1986, but compare van der Meijden 1989). Measurements of growth and survival of first-year rosettes of *G. crinita* along the transect and in the north and south transplant plots in the Radio Lab field suggest that there may be some density-dependent effect. However the rosettes in areas where they were relatively dense were often tiny (median diameter only 17 mm after a full season's growth, in the highest density class), and it seems unlikely that they significantly overlapped in terms of their spatial resource exploitation. Also the density of the much larger second-year plants, which also have a basal rosette, did not appear to affect survival of first-year plants in the south plots at the Radio Lab field. The effect of distance to nearest neighbor could be further studied, but it seems likely that plants would have to be very densely packed before suffering significantly from intraspecific competition. Certainly in the greenhouse even overlapping rosettes appeared to grow well, a feature noted by Sempers (1905a), who remarked that first-year rosettes did not appear to suffer much from close crowding and indeed grew best when the soil surface was entirely covered by the rosette leaves.

Herbivory

Damage to *G. crinita* due to herbivory did not appear to significantly affect survival of vegetative plants in established populations. However it would be preferable to confirm this in the future by carrying out experiments rather than relying on observations, which often cannot provide definitive answers on cause of mortality. When investigating the effect of herbivory on rare versus common species, Landa and Rabinowitz (1983) found that rare rather than common prairie grasses were preferred by a grasshopper. *D. carota* may well suffer less from herbivory than *G. crinita* as it is an introduced species in North America (Chapter 2) and may lack the herbivores present in native populations. When in the reproductive stage, *G. crinita* certainly seemed to suffer more damage than *D. carota* (Chapter 4). However it was not possible in my study of vegetative survival and performance to assess whether the rare *G. crinita* was more preferred than the common *D. carota* as the latter was found to have greater turnover of leaves so the evidence of damage could disappear. In contrast, *G. crinita* rosettes kept their leaves throughout the growing season.

The poor survival and reproductive output of the transplants at Turkey Hill (a site where *G. crinita* was not found naturally) suggest that herbivory could exclude *G. crinita* from certain habitats, perhaps those that are relatively fertile and productive and capable of supporting large populations of herbivores. Parker and Root (1981) showed that a biennial forb found in western North America (*Machaeranthera canescens*) was excluded from some areas because of herbivory by a grasshopper species. However the picture was complicated by the fact that exclusion only occurred where another food plant of the grasshopper was present.

Interactions among factors

Parker and Root's example again raises the important issue of interactions among factors limiting populations. As mentioned in Chapter 3 (Section I), interactions such as that between competition from woody species and low nutrient levels may limit *G. crinita* populations. The behavior of *G. crinita* in the investigations described in this chapter may well involve other interactions and parallel those

found in studies of other species, for example the interaction of interspecific competition and soil factors, especially moisture (Moloney 1990), and the interaction of defoliation by herbivores and level of nutrient supply to the plant (Verkaar et al. 1986).

Mortality of *G. crinita* may be more severe in areas with inconstant moisture supply where there is greater competition from other plants. This may be the case in the northern section of the transect in the Radio Lab field, where plant cover was greater than in the wetter southern part, although in fact soil moisture and plant cover were not correlated along the transect in 1989. Effects of damage by herbivores may be less where nutrient supply is greater, for example in the northern section of the transect where the supply of potassium is greater than in the southern part. However a great deal of further work would be required to fully elucidate all these relationships.

From the point of view of practical conservation management, useable guidelines for the selection of sites to conserve existing populations or for re-introduction would appear to be (1) that sites have an adequate moisture supply that is relatively constant year to year and (2) soils are circumneutral to alkaline and preferably relatively infertile. In sites with no natural disturbance regime, this might mean that less active management would be required to keep woody plants in check and also that likelihood of herbivore damage might be lessened.

Habitat specialization, physiological and ecological performance optima, and population refuges

The difference in relative abundance of *G. crinita* and *D. carota* appears to result at least in part from the greater "habitat specialization," in terms of edaphic factors, by *G. crinita*. Other workers have also found evidence of the association of habitat specialization and rarity. Rabinowitz et al. (1986) found that most rare species, in a sample from the British flora, were widespread geographically, had a restricted habitat, and high local population size. Hodgson (1986a), in a study of the flora of the Sheffield region of central England, found that rare species were more restricted to a narrow range of habitats than common species. However, care needs to be exercised in defining what "habitat" means and what is special about it. Rabinowitz et al. (1986) and Hodgson (1986a) appear to use vegetation type, for example marsh, woodland, and heath, as synonymous with habitat. Vegetation type can be misleading though; for example the bluebell, *Endymion non-scriptus*, is found in Britain in woodland, rough grass, bracken, and among rocks or on rock ledges (Blackman & Rutter 1954). However it is sensitive to drought and occurs outside woodland more commonly in the regions of higher rainfall in north and west Britain (Blackman & Rutter 1954). Thus it would have wide habitat breadth in terms of vegetation type, but rather narrow specialization with regard to moisture requirements. Similarly, *G. crinita* occurs in a relatively broad range of vegetation types, such as old field, prairie, marl marsh, and landslips, but is limited to a relatively narrow set of moisture conditions.

A number of studies have referred to the importance of edaphic factors in explaining rarity (Welsh 1979, Gehlbach & Polley 1982, Brown 1984, but see Burgman 1989). Hodgson (1986a) found that, like *G. crinita*, rare species in the Sheffield area were generally associated with infertile sites, which often had calcareous soils. Kruckeberg and Rabinowitz (1985) noted that endemic species are often associated with unusual substrates such as serpentine and limestone. However they also pointed out that such species were often not physiologically restricted to these substrates, for instance mangroves do not require saline conditions but can tolerate salinities that exclude other species. This characteristic of rare species may be a more pronounced manifestation of a phenomenon that has been well-studied, that is, the difference between physiological and ecological performance optima. Plant species have been found to grow equally well or better, under experimental conditions or as transplants, outside what appears to be the optimal ecological conditions in the field (Hackett 1965, Byer 1969, Sharitz & McCormick 1973, Pickett & Bazzaz 1978, Rabinowitz 1978b, Austin & Austin 1980, Huiskes & Steinstra 1985). Generally the difference in performance has been attributed to

competition (Sharitz & McCormick 1973, Pickett & Bazzaz 1978, Austin & Austin 1980), but dispersal characteristics have also been suggested (Rabinowitz 1978b).

Superficially *G. crinita* appears to be a similar case in that it is generally found in the field in soils over pH 7, but grows best on mildly acid soil in the greenhouse. However the Radio Lab studies show that the "ecological optimum" in terms of survival, growth, and reproductive output is not static; rather, it is dynamic and can shift spatially and temporally. In wet years the optimum is in the northern part of the Radio Lab field, in drier years it shifts to the south. *G. crinita* may best be described as an "edge" species, occupying a narrow and dynamic zone between dry and very wet situations where moisture conditions are more constant. Distribution along "edges" may be a more general characteristic of rare species. Hodgson (1986a) noted that many rare species in the Sheffield region were found in edge zones between habitats.

Several biennials have been found to exhibit spatial shifts in peaks of abundance (Batty et al. 1984, Grubb 1986, Kelly 1989c). Grubb (1986) describes these patterns as "drifting clouds of abundance," for which a wide variety of causes can be proposed, such as build-up of predators or pests, a persistent seed bank, random effects of dispersal or different sward heights (Batty et al. 1984, Grubb 1986). The patterns of abundance may reflect differing habitat quality across a site, for example van der Meijden (1989) found that shaded areas provided refuges for *Senecio jacobea* on dunes in The Netherlands, where it could persist when drought and defoliation by the cinnabar moth (*Tyria jacobaeae*) greatly reduced the originally more abundant populations in the open. Kelly (1989c) suggested that different areas in chalk grassland in England might provide the best habitat in different years for *Gentianella amarella* though these refuge areas might not be constant in space, leading to the "shifting cloud" phenomenon.

Shmida and Ellner (1984) and Pulliam (1988) argued that the occurrence of refuges or "source-sink" conditions may be widespread, though there seems to be a dearth of actual examples for plant species. Populations may persist in "sink" habitats where within-habitat reproduction is insufficient to balance mortality, because of continued immigration from "source" (refuge) areas. In the case of *G. crinita*, the northern end of the Radio Lab field can be seen as a "sink" where mortality is sometimes very high and re-establishment of a population may require immigration of seeds from the southern "source" part of the field. Similarly, outlying populations around a core area, for example as found along roadsides near the Radio Lab field, may become established in favorable years. But they will prove to be ephemeral if re-colonization from the core or "source" population does not occur after a dry season, during which the outlying "sink" populations become extinct.

Pulliam (1988) pointed out the importance of identifying the source population if a species is to be conserved in a particular area. My study has shown how misleading short-term assessments of relative performance can be, as *G. crinita* may grow larger and produce more flowers in areas where it cannot survive over a longer time scale, while an area containing low-growing individuals with few flowers may constitute the core population. Conservationists need to be careful, when they select site boundaries, that they either monitor the population over years that cover marked fluctuations in moisture supply or that they make a detailed assessment of the range of moisture conditions and nutrient levels across the site.

Presumably common species like *D. carota* have larger source areas, but it would be interesting to know whether the extreme fluctuation in performance between different years in "sink" and "source" areas is characteristic only of rare species, i.e. whether common species always do better in their "source" or refuge areas than in "sinks." The example of ragwort (*Senecio jacobea*; van der Meijden 1989), a common weed, suggests this may not be the case. Its refuge seems to be less favorable sometimes than the sink areas.

For practical conservation purposes, the selection of sites for the long-term conservation or re-introduction of populations of *G. crinita*, and the definition of site boundaries needs to be very carefully done. In particular, sites should include as far as possible a complete gradient of moisture conditions from very wet to dry so that the population can shift along the gradient depending on temporal variation in moisture supply.

CHAPTER 6

SUMMARY AND CONCLUSIONS

VALUE OF THE STUDY: SPECIFIC AND GENERAL CONCLUSIONS

The use of a comparative life history approach in my thesis, when organized around a framework of generalizations about biennials, did provide specific answers to the question of why *G. crinita* is rare. The approach would be worth repeating for other species from the biennial group or for representatives of other life history groups. *G. crinita* performed as well as a common biennial, *D. carota*, in relation to several of the generalizations that describe a "successful" biennial life history and the habitats where biennials usually occur. However the relative scarcity of *G. crinita* compared to *D. carota* appeared to derive at least in part from *G. crinita*'s lower survival in the vegetative stage because of its greater edaphic specialization. The role of herbivory in reducing survival and the effect of competition in waterlogged habitats may also be significant and need further study. The generalizations about biennials, hypotheses derived from them and conclusions reached about *G. crinita*'s rarity are summarized in Table 6.1. Work that could be done in the future to fill in gaps in the picture is outlined in Table 6.2. Brief comments on the wider ecological relevance of the study are followed in this chapter by a synthesis of the results of the project and other relevant information. The synthesis was produced in an attempt to throw light on the problems of how *G. crinita* came to be rare and what might happen to it in the future. The chapter concludes with a summary of recommendations that attempt to define what practical steps can be taken to conserve populations of *G. crinita*.

Table 6.1. Summary of generalizations about the life history of biennials, hypotheses derived from them and conclusions reached about the reasons why *G. crinita* is rare.

a	Generalization:	Biennials appear in early to mid-successional habitats, in local patches of bare ground or in more or less closed swards of herbaceous vegetation and may persist for some time.
	Hypothesis:	<i>G. crinita</i> can only survive through a short part of a successional change from bare ground to forest (Chapter 3, Section I).
	Conclusion:	<i>G. crinita</i> can survive in a similar range of successional habitats as the common biennial, <i>Daucus carota</i> , and can even survive and reproduce in mid-successional stages dominated by tall herbs and low shrubs. <i>G. crinita</i> may have lower survival than <i>D. carota</i> in early to mid-successional habitats but may have a higher potential reproductive output. However neither <i>G. crinita</i> nor <i>D. carota</i> can survive in later, shrub-dominated stages.
	Hypothesis:	<i>G. crinita</i> is restricted in abundance by a scarcity of suitable microhabitats for colonization and regeneration, in the successional habitats where it can survive (Chapter 3, Section II).
	Conclusion:	<i>G. crinita</i> does not require a specific, uncommon microhabitat for successful regeneration. It can be favored by a greater abundance of particular microhabitats, i.e. bare ground and moss, though the presence of large expanses of bare ground does not automatically mean that <i>G. crinita</i> will be abundant. It can survive well in a fine-grained mosaic of bare ground, moss, vegetation and litter. It does not appear to be consistently more limited than <i>D. carota</i> in the range of microhabitats that it favors, indeed it sometimes appears to be less demanding than the common biennial.
b	Generalization:	Biennials are successful at colonizing intermittently available habitats and have efficient seed dispersal in time or space.
	Hypothesis:	<i>G. crinita</i> has limited colonizing ability because of poor seed dispersal capabilities (i) in time (ii) in space (Chapter 3, Section III).
	Conclusion:	<i>G. crinita</i> appears to lack a long-term seed bank and requires habitats that remain permanently open to persist in a locality without immigration of seed from elsewhere, but so does the common biennial, <i>D. carota</i> . <i>G. crinita</i> seems to have a similar potential for spatial dispersal as other species, although the role of animal dispersal is unclear. Dispersal by water may be important and <i>G. crinita</i> does not appear to be scarce because of any obvious lack of ability to disperse over long distances.
c (i)	Generalization:	Biennials have a high reproductive output.
	Hypothesis:	The relative scarcity of <i>G. crinita</i> is due to the low reproductive output of adult plants (Chapter 4).
	Conclusion:	<i>G. crinita</i> has a higher reproductive output than the common biennial, <i>D. carota</i> .

Table 6.1 (continued)

c (ii)	Generalization:	Biennials have good survival in the vegetative stage.
	Hypothesis:	In unwooded landscapes, the survival, growth and potential reproductive output of <i>G. crinita</i> in the vegetative stage are limited by a narrow range of soil conditions (Chapter 5).
	Conclusion:	Although the distributions of <i>G. crinita</i> and <i>D. carota</i> overlap, and <i>G. crinita</i> can sometimes grow well in areas with abundant <i>D. carota</i> , <i>G. crinita</i> appears to be limited by a narrower range of edaphic factors than <i>D. carota</i> , particularly with regard to soil moisture. Competition from tall, robust, herbaceous plants in waterlogged sites, increased herbivory in areas with fertile soils, and other interactions between soil factors, competition and herbivory may also be important and deserve further attention.

Table 6.2. Topics for future studies on the ecology of *G. crinita*.

1. Further study of the effect of ground disturbance on the emergence of *G. crinita* seedlings from the seed bank, to discover if continual disturbance consistently increases the emergence of seedlings from seeds shed two or more years previously.
 2. Assessment of the role of animal and human agencies in seed dispersal, particularly their role in linking sites by enabling colonization and recolonization to occur, although this is recognized to be a very difficult subject to investigate.
 3. Investigation of the variability in reproductive output in relation to seasonal events such as droughts, and the impact of damage, caused by herbivory or mowing, on second year plants. In particular the quality of seed that is set in drought years or in flowers that have developed after damage deserves study.
 4. The circumstances under which adequate compensation in flower production after damage occurs, perhaps as part of a more general investigation of the impacts of various levels and timing of deer and domestic stock grazing or impacts of timing and frequency of mowing on reproductive output.
 5. The role of competition from robust herbaceous plants in excluding *G. crinita* from waterlogged sites, and the effects of subtle interactions between soil factors, competition, and herbivory. Interactions of particular interest would seem to be those between soil nutrient levels and available light in shaded situations, competition from herbaceous plants and soil moisture levels in dry conditions, and amount of herbivory and soil nutrient supply.
 6. The extent of underlying genetic variation within the species and the possible existence of ecotypes. This work would guide action to conserve genetic diversity. It would also aid assessment of the applicability of my findings about populations in New York State to other populations across *G. crinita*'s range in North America.
-

The study pointed to several topics that would be worth investigating further in the search for general patterns underlying the ecology of rare species. A fruitful line of investigation might be a comparison of the germination behavior of rare and common species to try to discover if rare species tend to be relatively non-specific in their response to germination cues in comparison to common species. Such behavior could result in a higher proportion of seedlings of rare species emerging from the seed bank in places where they cannot survive compared to the proportion of seedlings of common species that emerge in these situations. Perhaps other rare species apart from *G. crinita* suffer from this combination of two traits, i.e. unspecialized germination behavior and specialized requirements for survival in the vegetative stage. For instance *Gentianella germanica* seedlings do seem to emerge in situations where they cannot survive (Schenkeveld & Verkaar 1984).

An assessment of the importance of phylogeny in underlying this pattern of rarity and other traits of rare species may prove to be illuminating. Some families do seem to have a disproportionate number of rare members. For example in the British flora, among the 32 families in the flora which have more than 10 species, the Gentianaceae family has the second highest proportion of rare and scarce species (69% compared to an average of 35%; Fumariaceae had the highest proportion, 73%; data from Clapham et al. 1987 and Nature Conservancy Council 1989). The Gentianaceae family also has a relatively high proportion of short-lived monocarpic species (81%, including 4 rare and scarce species in the genus *Gentianella*) compared to perennial species, whereas in the British flora as a whole the proportion is only 32%. These relationships between rarity, phylogeny, and life history deserve further investigation in the search for patterns in the ecology of rare plants.

Further investigations of the role of source or refuge areas in allowing rare populations to persist would be valuable, as well as examination of whether other species exhibit the phenomenon of shifting ecological optima in the field. Another interesting question concerns the relative performance of common and rare species in source and sink areas. Do rare species show more extreme fluctuations in performance in these two areas, compared to common species? In addition, more studies on the related issue of dynamics of patches of habitats may take the understanding of rarity beyond that supplied by plant population dynamics alone.

Other topics that deserve more work and which my study touched upon briefly are the role of herbivory in limiting the distribution of rare species, and relative reproductive output and its variability among rare and common species.

SYNTHESIS: *G. crinita* POPULATIONS IN THE PAST, PRESENT AND FUTURE

An understanding of how a species has become rare can assist in the task of conserving it now and in the future. The following assessment of *G. crinita*'s past distribution and abundance, current status, and future prospects is aimed at helping conservationists to understand the "history" of *G. crinita* and how its past may affect attempts to conserve the species. The assessment is based on a synthesis of the findings described in Chapters 2 through 5, and relevant information on vegetation and land use changes that have happened in the North American landscape since the time of the last glaciation some 20,000 years ago.

It seems that *G. crinita* is a species that would have been ideally suited to conditions that were probably widespread in the late-glacial period in eastern North America, that is, open, unwooded habitats with wet, disturbed, mineral soils relatively high in bases such as calcium. After the ice retreated, around 18,000 to 19,000 years ago in New York State and New England (Muller et al. 1988, Miller 1990), and before forest cover developed around 12,000 to 9,000 years ago, tundra vegetation predominated. It was characterized by bryophytes, herbaceous vascular plant species, and low shrubs such as dwarf birch and alder (Davis & Jacobson 1985, Miller 1990). However the vegetation was probably not as shrubby as tundra today (Davis & Jacobson 1985). Evidence provided by fossil seeds has shown that *Gentianopsis* (either *G. crinita* or *G. procera*) was present during this time (Miller 1989). It is likely that substrates would have been very unstable in a zone along and near the ice margin. Geomorphological processes such as frost heaving and slumping of saturated sediments over permafrost would have been widespread in periglacial areas around the edge of the ice sheet in the northern hemisphere (West 1968, Godwin 1975, Davis 1983). This ground disturbance would have kept unleached mineral substrates that were relatively high in bases, including calcium, in constant supply and would have hampered tree colonization (Godwin 1975). The flora present during the late-glacial period in eastern North America and elsewhere in the northern hemisphere reflected these conditions, as it appears to have been dominated by light-demanding, herbaceous species and bryophytes that can grow on calcareous substrates (Pigott & Walters 1954, Godwin 1975, Miller 1989, 1990). As well as lack of forest cover and an abundance of base rich soils across the landscape, wet conditions would have been prevalent. Marshy low ground and slopes "flushed" with free-flowing water were probably widespread (Miller 1973, 1990, Godwin 1975). In addition, severe floods of seasonal meltwater were likely to have been frequent (Godwin 1975).

From this evidence and the findings of my project it seems that the requirements of *G. crinita* for circumneutral to calcareous, wet substrates and lack of tree cover, together with its ability to regenerate in bare ground, moss, or herbaceous vegetation, would have fitted well with the conditions and vegetation types that appear to have been prevalent in the late-glacial period. *G. crinita* would not have needed a long-term seed bank as suitable habitats were plentiful and always available. Perhaps "blanket" germination of seed, which was unresponsive to variation in the "safety" of particular sites for survival in the subsequent vegetative stage, might not, therefore, have been a serious disadvantage.

Wet, continuously unstable landslips such as at Letchworth probably provide the closest analogy among the current habitats of *G. crinita* to those that it occupied in late-glacial times.

G. crinita's current range is largely within the part of North America that was once glaciated (Fig. 6.1) and it must have spread from unglaciated refuges once the ice sheet retreated. Godwin (1975) thought that the late glacial might have been a time of extremely rapid spread by herbaceous species because of the abundance of open habitats. *G. crinita* could have spread quickly especially if, as Iltis (1965) suggested, populations were locally enormous at this times. Dispersal of seed by cold meltwater might have been of particular significance for *G. crinita*. In my study, seedling emergence was not prevented by first immersing or floating seeds in cold water, before sowing them on a moist substrate; indeed these treatments provided effective stratification techniques.

Around 12,000 years ago spruce and pine forests began to extend across eastern North America (Davis 1983). Miller (1973, 1989) suggested that the development of forest cover and associated soil changes, in particular acidification through leaching and litter accumulation, severely restricted the distribution of the light-demanding herbaceous plants and bryophytes that grew on circumneutral or calcareous soils. *G. crinita* would have suffered in this way given that it had these ecological requirements, perhaps primarily through shading by trees rather than from soil changes which were probably very gradual. Its range now lies almost entirely within the forest zones of eastern North America (Fig. 3.9) so it has lost most of its previously unwooded territory. It is not clear why *G. crinita*'s range does not extend farther north into present tundra areas. It appears to have been "caught up" by the spread of the forest northwards or perhaps the habitat or climatic conditions in present tundra latitudes are in some way unsuitable.

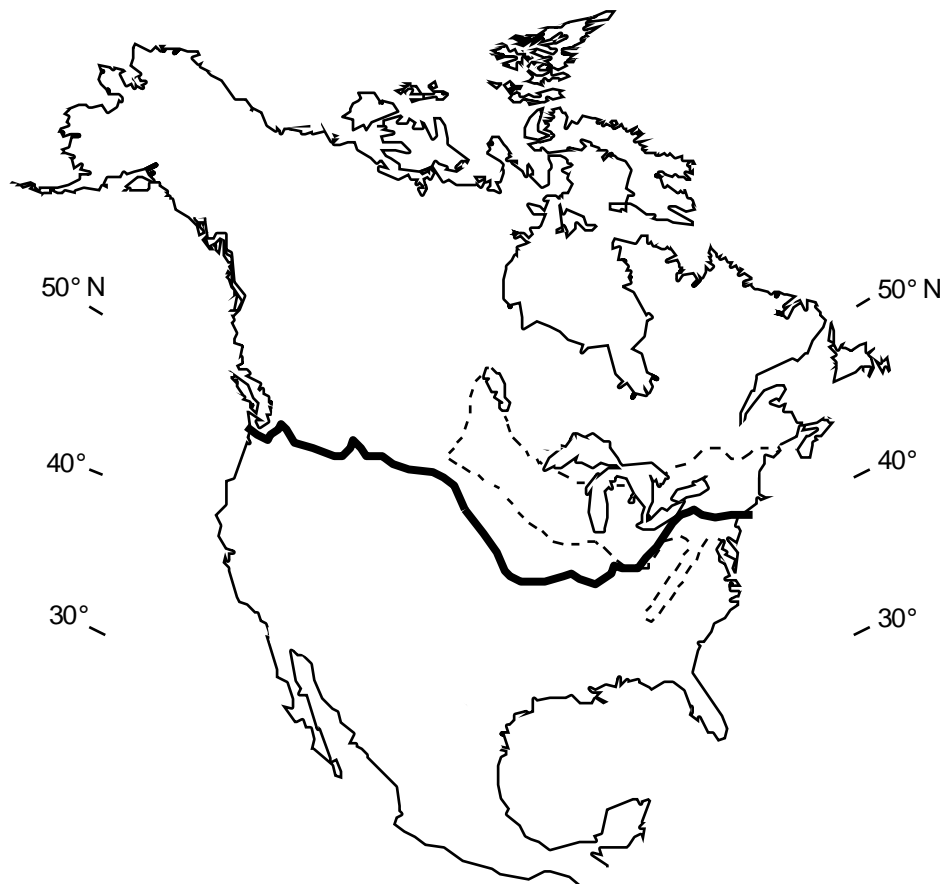


Fig. 6.1. Range of *Gentianopsis crinita* (- - -) in North America in relation to the limit of maximum glaciation (—). Adapted from Iltis (1965).

The next question to arise is in which habitats did *G. crinita* populations survive when forests covered most of the landscape in the post-glacial period? Indeed where did *G. crinita* survive in previous interstadials between earlier glaciations? Evidence suggests that suitable, relatively permanent, unwooded habitats were very scarce in eastern North America during the post-glacial period. For example, survey records made in Tompkins County, central New York in 1790-91, before extensive European settlement occurred, showed that only 0.16% of the surveyed distance was not forest or regenerating forest (Smith et al. *in press*). Of this small percentage, "meadow" made up 0.02%, marsh 0.05%, and alder thicket 0.09% (Drs. P. L. Marks and S. Gardescu, Cornell; pers. comms.). All three could potentially have supported *G. crinita* populations if they had been wet enough and sufficiently open. Marks and Gardescu (1992) found that in the 1790's, 1.4% of the surveyed distance in the central Finger Lakes Region of New York, including part of Tompkins County, was recorded as marsh, meadow, or wet shrub thickets. In western New York, survey records from the late 1700's to early 1800's indicated that rather larger percentages of the surveyed distance there were unforested, but even so, more than 95% of the landscape was forested (Seischab 1990). Seischab found that "grass" occupied 0.6% of the surveyed distance, marsh 1.8%, and "shrubs" 1.5%, while agricultural fields made up 0.3% of the surveyed distance. Widespread occurrence of *G. crinita* in temporary forest openings, say after treefalls, would have been unlikely as it appears to lack a long-term seed bank.

Natural, more or less permanently open habitats in the forested landscape that were capable of supporting *G. crinita* populations probably included landslips, unstable river banks where material was eroded or deposited, marl marshes, beaver meadows, and fragments of prairie. The suitability of landslips, such as that at Letchworth State Park, has already been discussed. River banks could have provided an interconnected series of sites, some of which were always open, in a similar way as they do now for the rare Furbish's lousewort, *Pedicularis furbishiae* (Menges 1988). This species occupies the dynamic riverbank habitat along the St. John River in Maine and New Brunswick. Here the populations of the lousewort behave as a metapopulation, i.e. a population of populations. The overall survival of the species depends on the rates of extinction and recolonization of the component populations, as governed by the frequency and severity of disturbance by ice scour and bank slumping (Menges 1988). The upper reaches of the Genesee River in western New York appear to be a stronghold for *G. crinita* and may represent a current example of a riverbank metapopulation. A series of populations occur along the river, including the one on the Letchworth landslip, and over recent years new populations have been noted while others have disappeared (D. Bassett, pers. comm.).

Open marl marshes, like those that are still present at Bergen Swamp and Mendon Ponds in western New York (Muenscher 1946, Goodwin 1943, Futuyma 1990) may also have provided a haven for *G. crinita*. *G. crinita* has been recorded at Bergen Swamp (Muenscher 1946) though it has not been seen recently (Dr. Pat Martin, pers. comm.), while I recorded it at Mendon Ponds during my study. Marl deposition appears to have made available a continuous supply of open habitats at Bergen. Over time, open marl areas have formed in flooded parts of the swamp that were once forest, and forest cover has re-established in marl areas that have become drier (Muenscher 1946, Futuyma 1990).

The activities of beavers in creating open habitats may have provided widespread networks of suitable habitats for *G. crinita*. Prior to the arrival of Europeans in eastern North America, nearly every lake, pond and stream was probably occupied by colonies of beavers (Naiman et al. 1986). Beavers provided open habitats in various ways. They felled trees, created ponds behind dams, trampled landing places beside streams and ponds, and sometimes made well-defined, worn and rutted trails along which logs were dragged (Warren 1927). "Beaver meadows" may have been the most significant habitat for *G. crinita* resulting from beaver activity. These meadows formed after the ponds made by beavers filled in with sediment or when dams were abandoned and the ponds drained away. The vegetation of the meadows sounds reasonably suitable. Morgan (1868) described them as being

covered with tussocks of coarse grass surrounded by narrow strips of bare and sunken ground. Shanks (1966) recorded marsh meadow habitats, composed of tussocky grasses and sedges, as especially characteristic of beaver-dam sites in Monroe County, western New York. Paine (1865) actually recorded the presence of *G. crinita* from the borders of beaver meadows in Oneida County, central New York. Some meadows could have remained open for a considerable time, perhaps even centuries (Naiman et al. 1986). Beavers may also have played a significant role in the long-distance dispersal of seed in mud clinging to their fur or feet, particularly when they colonized new sections of river systems or new catchments and in the same way also enabled local recolonization by *G. crinita* to occur. Long-distance dispersal of seed by beavers could have been relatively rapid. Johnston and Naiman (1990) estimated that beavers could colonize across a distance of 736 km in just 46 years from an initial nucleus in northern Minnesota, although in this case, beavers would have been moving into an area of "empty" habitat without existing beaver populations.

Fragments of prairie, or "oak openings," which now support *G. crinita* populations in Ohio (Easterley 1979) and western New York (my study) could have been significant for the survival of *G. crinita* in the forest period. Native Americans may have played a part in keeping such fragments open, for instance by burning them to encourage game (Severinghaus & Brown 1956). The "grass" areas recorded in the late 1700's and early 1800's in western New York were probably cleared by Native Americans (Seischab 1990).

The spread of European settlement into eastern North America had enormous effects on the landscape. The impacts relevant to *G. crinita*'s distribution and abundance were double-edged. On the positive side, large tracts of forest were cleared. For example in Tompkins County, forest cover dropped from nearly 100% in 1790 to only about 19% in 1900 (Smith et al. *in press*). Humans may also have played a part in dispersing *G. crinita* seeds into fields and along roadsides. Deer, which can be damaging grazers of second-year *G. crinita* plants, but may also occasionally facilitate seed dispersal, were greatly reduced in numbers and even extirpated in some places by the late 1800's, for instance in western and central New York (Severinghaus & Brown 1956). On the more clearly negative side, beavers were almost wiped out by 1900 in North America (Naiman et al. 1986) and their habitats lost. Marks and Gardescu (1992) found that evidence of beaver activity was rarely recorded in the 1790's survey of the central Finger Lakes Region, and suggested that intensive trapping had already greatly reduced beaver populations. Beaver meadows may have often been the first land to be taken over by settlers to provide pasture, hay and crops because they were level, open and fertile (Warren 1927). Naiman et al. (1986) estimated that from 1834 onwards some 195,000 to 260,000 square kilometers of beaver habitat in marshes, swamps, and seasonally flooded bottomlands were converted to dry land in the United States. Engineering work along rivers, for instance artificial channel stabilization and embankment, may also have reduced *G. crinita*'s habitat. As described in Chapter 2, flower picking in the late 1800's and early 1900's could have further reduced populations.

G. crinita has taken advantage of habitats created by humans, as already demonstrated in Chapter 5. A survey of *G. crinita* localities in New York State showed that the plant occurred in various artificially disturbed and/or managed localities, including old fields, roadsides, and sand, gravel or marl extraction sites. However *D. carota* has been able to make far better use of these new open habitats. It was able to become common and widespread in North America just 300 years since it was first introduced. Griggs (1940) suggested that many rare species in North America did not spread fast enough to take advantage of clearances made by humans, in contrast to the common species which shared their early successional habitats. In the case of *G. crinita*, its narrower edaphic tolerance, particularly with regard to soil moisture, and perhaps greater susceptibility to herbivory, may partly explain its inability to match *D. carota*'s capacity to take advantage of human activity. On a small scale, this is demonstrated by the studies in the Radio Lab field which showed that while *D. carota* could maintain its "occupancy" across the whole field and therefore seed-bearing plants were present all the way across it, *G. crinita* was only able to survive in the longer term in a part of the field, and seed had to recolonize from sources farther away. Edaphic specialization could also have affected

the relative numbers of seeds of *G. crinita* and *D. carota* that dispersed over long distances. *D. carota* would have had a larger extent of suitable habitat in any one area in the landscape because of its wider edaphic tolerance. Its populations would therefore most probably have been much larger and produced more seeds than populations of *G. crinita*, although *D. carota*'s advantage would have been offset to some extent by *G. crinita*'s greater seed output per plant (Chapter 4). Thus if smaller *G. crinita* populations did produce fewer seeds and if the two species generally had the same proportion of seed dispersing over long distances to suitable habitats, for example 1% of the seed output, more individual seeds of *D. carota* would have reached these habitats.

During the later years of the twentieth century, there have been further changes in land use and wildlife populations that are relevant to *G. crinita*. Forest cover has increased again in eastern North America as farmland has been abandoned. By 1980, about 50% of Tompkins County in central New York was forested, which represents a 30% increase since 1900, and similar trends have been found elsewhere in the region (Smith et al. *in press*). Deer populations recovered (Severinghaus & Brown 1956, 1970) and beaver colonies spread once again although beaver populations are still only a small fraction of earlier numbers (Naiman et al. 1986). Also the frequency of *G. crinita* populations may have been directly increased by the deliberate spreading of seed in the wild, as discussed in Chapter 2.

At present, in many states across *G. crinita*'s range, drainage of wetlands and forest regrowth are seen as the major threats to the species (Heritage Programs, pers. comms.). Forest regrowth appears to be a particular problem in eastern states, for instance endangered populations in Maryland, Virginia and North Carolina are threatened by spread of woody species (Heritage Programs). For the 32 sites surveyed in New York State (Chapter 5), succession to scrub and forest is likely to be an imminent problem in 6 sites (unmanaged old fields) and in 10 to 15 years if mowing or grazing ceased in 13 other sites. The problem is demonstrated at a local scale in the Ithaca area where the *G. crinita* population in the Natural Area has declined over the last 20 to 30 years and scrub now covers most of the preserve (see Chapter 2).

In light of this review of *G. crinita*'s past and present status, *G. crinita* can probably be regarded as a rare relict from a time when it was much more abundant. However, before European settlement it appears to have been a resilient relict as it survived through several thousand years in a landscape dominated by forests, despite populations being small and scattered because suitable habitats were limited in area and infrequent. The degree of isolation of these populations may have been critical. The resilience of *G. crinita* may have resided in the fact that populations were interconnected by river systems and/or beaver activities or deer movements and thus recolonization after local extinction was possible. *G. crinita*'s continued survival may depend on how far human activities have eroded the viability of this pattern through habitat destruction and disruption of natural interconnecting links between populations, as against some increase in suitable habitat by forest clearance and perhaps some facilitation of seed dispersal. Conservationists may now have to deal primarily with the tricky problems of trying to preserve remnants of networks and isolated populations.

The findings of my project indicate that, especially for the long-term conservation of isolated populations, the persistence of *G. crinita* not only depends on the prevention of forest re-growth or wetland drainage, but also on the "quality" of the site itself in relation to environmental fluctuations, in particular those affecting soil moisture. Long-term "core" or "refuge" localities must have an adequate moisture supply even during droughts. An illustration of how important long-term quality might be is given by the history of *G. crinita* at the Radio Lab field. *G. crinita* has been known to have been present at this site for 20 years (see Chapter 2). The 1988 drought roughly halved the habitable area for *G. crinita* although it was classed as a "mild drought" by Knapp and Eggleston (1989). They used the Palmer Drought Severity Index to reach this conclusion. The Index is calculated on the basis of abundance of precipitation in relation to the losses such as runoff and evapotranspiration. The period 1980-83 had similar Index values as 1988 and *G. crinita* apparently survived. However the 1950's and

1960's had "severe droughts" and in the period 1895-1988, 38 years were at or below the Index value for 1988. Thus *G. crinita*'s survival would probably have been somewhat precarious over this longer period. *G. crinita*'s sensitivity to drought means that risks of local extinction of a population will depend more on the "quality" of the patch rather than any "minimum viable population size." Shaffer (1981) defined "minimum viable population size" as a population that is large enough to maintain itself under average conditions and also of sufficient size to survive perturbations over time. In catastrophic droughts, no population of *G. crinita* is large enough to ensure that some individuals survive. For example in the fall 1991 after a severe drought during the growing season, no flowering *G. crinita* were recorded at the Radio Lab field (Dr. Nancy Ostman, Cornell University; pers. comm.), where thousands had been present two years before.

Against the background of *G. crinita*'s past and present status what judgements can be made about its future? Three possible scenarios can be envisaged apart from maintenance of the status quo. The current frequency of populations of *G. crinita* across its range appears to peak in the midwestern states of Wisconsin, Michigan and Indiana and tail off in the states to the northwest, east, and southeast (Fig. 2.3). Frequency of populations also declines in states to the southwest, but information for Canadian provinces to the northeast is limited (Fig. 2.3). A hypothetical, two-dimensional representation of the change in frequency of populations across *G. crinita*'s range from northwest to southeast is shown in Figure 6.2, together with three possible ways that this distribution might alter in the future (Fig. 6.2a-c).

The first scenario of a collapse in range of *G. crinita* would result from a continuation of current trends in habitat loss together with random environmental fluctuations that extinguish isolated populations. Both factors would operate across the whole range so that the remnant range would be centered on the stronghold states where populations were once most frequent. However even here the number of localities would fall (Fig. 6.2a). The second scenario depicts a more likely contingency, i.e. strenuous conservation efforts are directed towards maintaining the localities in states where *G. crinita* is on the endangered species list, while a "levelling down" occurs in states where no protection is afforded the plant (Fig. 6.2b). The third scenario is the most speculative but also the most intractable. If significant climatic change occurs over the next fifty years or so, for instance if there is a shift to warmer and drier conditions, the range of *G. crinita* may become truncated (Fig. 6.2c). This scenario assumes that little successful natural dispersal northwards will occur. Populations would be especially at risk in those sites in the south that have a limited range in moisture conditions.

Human activities have already substantially interfered with *G. crinita*'s natural distribution and abundance. It seems likely that conservationists will have to continue to interfere in order to try to stem declines in frequency of populations resembling those described in the above three scenarios for the future. My project has produced specific conservation recommendations, summarized below, that are aimed at helping conservation managers to maintain populations in existing sites and identify suitable sites for re-introduction or introduction. Where detailed knowledge of particular issues is lacking, for instance on genetic variation within the species, the recommendations try to define the safest course of action.

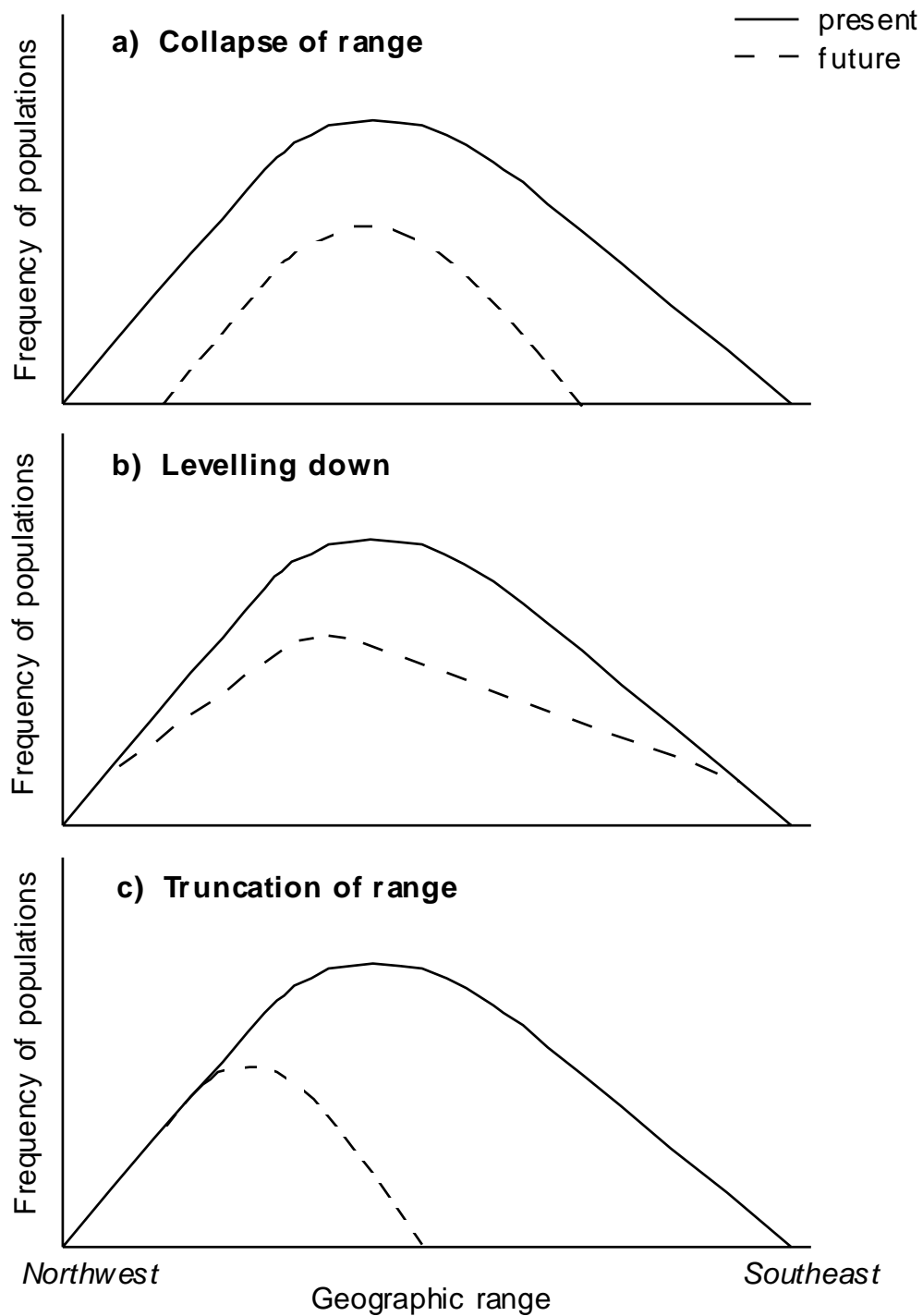


Fig. 6.2. Three scenarios of possible future changes in the frequency of populations of *G. crinita* across its range in North America, represented by hypothetical curves of changes in frequency along a swath running northwest to southeast across the United States.

SUMMARY OF CONSERVATION RECOMMENDATIONS

1. Sites which are not kept open naturally, for example old fields or pastures (in contrast to landslips and other naturally open habitats), need continued, active, management to prevent encroachment by woody plants and development of a closed shrub and tree cover under which *G. crinita* cannot survive. Introduction into sites that are naturally open is likely to prove less costly in management terms than introduction into sites that require active management.
2. Localities that require management to control the spread of woody plants must be kept permanently open because *G. crinita* does not appear to have a reliable long-term seed bank.
3. Mowing or grazing vegetation to ensure that herbaceous plants predominate will allow *G. crinita* to survive even without deliberate ground disturbance. However, some disturbance within the sward may encourage more seeds to germinate among those that did not do so in the spring immediately following dispersal.
4. Mowing should be timed to occur relatively early in the growing season, if possible before most buds on second-year *G. crinita* plants develop, although individual plants can compensate for loss of flowers by growing new ones after damage has occurred. Ideally mowing should not be done every year, in order to allow *G. crinita* to flower undisturbed in some years. This should reduce a potential risk of loss in quality of the seed set. Seed of lower quality might be produced if most flowers originate from regrowth after mowing damage.
5. Grazing by cattle is not necessarily damaging to *G. crinita* populations and may control woody plants. Appropriate stocking levels would need to be worked out on a site by site basis, although clearly very heavy grazing and trampling, that led to destruction of *G. crinita* plants, would be damaging.
6. Damage by deer to flowering *G. crinita* may need to be evaluated in individual sites in areas where deer populations are high. Mitigation of damage may be achieved by further clearance of woody cover to discourage deer from remaining to graze on the site for long periods.
7. Give priority to conservation of populations in localities that have adequate long-term moisture supplies and if possible exhibit a complete gradient from dry to very wet conditions. Such sites can accommodate dynamic shifts in *G. crinita*'s distribution, survival, and performance along the gradient in response to fluctuations in moisture supply and spatial variation in nutrient supply. Inclusion of the entire moisture gradient in a site will help to ensure that a core part of the population can survive even in dry years. Be careful not to select site boundaries on the basis of what initially appears to be the "best" area for *G. crinita* in terms of the part of the site that has the largest plants with the most flowers. The core or refuge areas may have small plants with few flowers if soil nutrient levels in these areas are low.
8. Selection of a group of separate sites that have different moisture levels is a second option. It may be more risky but may sometimes be unavoidable. Artificial re-introduction may be required if natural recolonization does not occur after local extinction due to drought or flooding.
9. When all sites appear to be drying out over time (perhaps due to climate change), active management may be required to allow the populations to shift to wetter parts of each site. For instance, cutting of tall herbaceous swamp plants such as *Typha* (cattails) and removal of deep litter to encourage colonization and survival of *G. crinita* may be necessary, or ground excavation to the water table may be required to restore the gradient to wet conditions.

10. Choose sites for conservation, and especially introduction, that have infertile, circumneutral to alkaline soils. *G. crinita* does not appear to grow on acid soils. Colonization by woody plants may be slower on infertile soils and thus management costs can be reduced. In addition herbivore damage to *G. crinita* in infertile sites may be less. Introduction of *G. crinita* into sites that have been heavily disturbed, e.g. topsoil removed, is worth considering because these sites are usually infertile, and often have unleached substrates that can be relatively high in bases such as calcium.

11. At a regional level, if practicable, identify and conserve natural, interconnected networks of sites, for example, along river systems. These are likely to require minimum active management and support relatively resilient metapopulations of *G. crinita* over the long term, provided that they remain unaffected by developments such as engineering works for flood control.

12. At a regional and national level, conserve populations over as wide a geographic range as possible, and in a variety of habitats, to try to conserve at least some of the genetic diversity that might exist within the species.

APPENDIX I

SOURCES OF INFORMATION ON *Gentianopsis crinita*

i) HERITAGE PROGRAMS IN THE U.S.A. THAT PROVIDED INFORMATION ON *Gentianopsis crinita*:

Connecticut Natural Diversity Data Base	Nancy M. Murray
Delaware Natural Heritage Program	Leslie Trew
Georgia Freshwater Wetlands & Heritage Inventory Program	Tom Patrick
Illinois Natural Heritage Program	John Schwegman
Indiana Heritage Program	Mike Homoya
Iowa Natural Areas Inventory	Mark Leoschke
Kentucky Heritage Program	Marc Evans
Maine Natural Heritage Program	Trish DeHond
Maryland Natural Heritage Program	Lyn Davis
Massachusetts Nat. Heritage & Endangered Species Program	Bruce Sorrie
Michigan Natural Features Inventory	Mike Penskar
Minnesota Natural Heritage Program	Welby Smith
New Hampshire Natural Heritage Inventory	Frankie Brackley
New Jersey Natural Heritage Program	David Snyder
New York State Heritage Program	Steve Clements
North Carolina Natural Heritage	Alan Weakley
North Dakota Natural Heritage Inventory	Alexis Duxbury
Ohio Natural Heritage Program	Patricia Jones
Pennsylvania Natural Diversity Inventory, Eastern Office	Tom Smith
Pennsylvania Natural Diversity Inventory, Western Office	Paul Wiegman
Rhode Island Natural Heritage Program	Rick Enser
South Carolina Heritage Trust Program	John Nelson
South Dakota Natural Heritage	David Ode
Tennessee Department of Conservation	Paul Somers
Vermont Natural Heritage Program	Robert Popp
Virginia Natural Heritage Program	Christopher Ludwig
West Virginia Wildlife/Heritage Database	Paul Harmon
Wisconsin Natural Heritage Inventory	June Dobberpuhl

APPENDIX I (continued)

ii) HERITAGE PROGRAMS IN CANADA THAT PROVIDED INFORMATION ON *Gentianopsis crinita*:

Canadian Rare Plant Project, Ottawa, Ontario George Argus

Québec Direction du patrimoine écologique Francis Boudreau

iii) FLORAS REFERRED TO FOR INFORMATION ON *Gentianopsis crinita*:

(full citations given in References)

Andreas, B. K. and Cooperrider, T. S. (1981) The Gentianaceae and Menyanthaceae of Ohio.

Baldwin, W. K. W. (1958) Plants of the Clay Belt of Northern Ontario and Quebec.

Dore, W. G. and Gillett, J. M. (1955) Botanical Survey of the St. Lawrence Seaway Area in
Ontario.

Graves, C. B., et al. (1910) Catalogue of the Flowering Plants and Ferns of Connecticut Growing
without Cultivation.

Ilitis, H. H. (1965) The Genus *Gentianopsis* (Gentianaceae): Transfers and Phytogeographic
Comments.

Jones, G. N. (1963a) Flora of Illinois, 3rd edition.

Macdonald, H. (1977) Native Manitoba Plants in Bog, Bush, and Prairie.

Mohlenbrock, R. H. (1986) Guide to the Vascular Flora of Illinois.

Scoggan, H. J. (1957) Flora of Manitoba.

Seymour, F. C. (1982) The Flora of New England, 2nd edition.

APPENDIX II

SPECIES IN *Gentianopsis crinita* SITES

Frequency of occurrence of species in *G. crinita* sites. Most records are from surveys in 1989, and some are from other visits from 1987-89. () denotes a tentative species identification.

In 75-97% of sites

<i>Agrostis stolonifera</i>	<i>Daucus carota</i>	<i>Fragaria virginiana</i>
<i>Aster novae-angliae</i>	<i>Euthamia graminifolia</i>	<i>Prunella vulgaris</i>

In 50-74% of sites

<i>Aster lateriflorus</i>	<i>Leucanthemum vulgare</i>	<i>Ranunculus acris</i>
<i>Cornus foemina</i>	<i>Lotus corniculatus</i>	<i>Solidago canadensis</i>
subsp. <i>racemosa</i>	<i>Plantago lanceolata</i>	<i>Solidago nemoralis</i>
<i>Equisetum arvense</i>		

In 25-50% of sites

<i>Acer rubrum</i>	<i>Juncus tenuis</i>	<i>Rudbeckia hirta</i>
<i>Achillea millefolium</i>	<i>Lycopus uniflorus</i>	<i>Salix bebbiana</i>
<i>Anemone virginiana</i>	<i>Melilotus alba</i>	<i>Salix discolor</i>
<i>Asclepias syriaca</i>	<i>Panicum acuminatum</i>	<i>Scirpus atrovirens</i>
<i>Aster pilosus</i> var. <i>pringlei</i>	<i>Phleum pratense</i>	<i>Solidago gigantea</i>
<i>Aster sagittifolius</i>	<i>Picris hieracioides</i>	<i>Solidago juncea</i>
<i>Cornus sericea</i>	<i>Pinus strobus</i>	<i>Taraxacum officinale</i>
<i>Fraxinus americana</i>	<i>Plantago major</i>	<i>Trifolium pratense</i>
<i>Galium mollugo</i>	<i>Poa pratensis</i>	<i>Viburnum recognitum</i>
<i>Hypericum perforatum</i>	<i>Populus tremuloides</i>	
<i>Juncus articulatus</i>	<i>Potentilla simplex</i>	

In 5-25% of sites

<i>Abies balsamea</i>	<i>Carex hystericina</i>	<i>Eupatorium perfoliatum</i>
<i>Acer saccharum</i>	<i>Carex lurida</i>	<i>Eupatorium rugosum</i>
<i>Agrimonia gryposepala</i>	<i>Carex vulpinoidea</i>	<i>Geum aleppicum</i>
<i>Agrimonia striata</i>	<i>Centaurea nigra</i>	<i>Helianthus giganteus</i>
<i>Agropyron repens</i>	<i>Cerastium fontanum</i>	<i>Hieracium pilosella</i>
<i>Alnus incana</i> subsp. <i>rugosa</i>	<i>Cichorium intybus</i>	<i>Holcus lanatus</i>
<i>Ambrosia artemisiifolia</i>	<i>Clematis virginiana</i>	<i>Hypericum punctatum</i>
<i>Antennaria plantaginifolia</i>	<i>Clinopodium vulgare</i>	<i>Juncus balticus</i>
<i>Anthoxanthum odoratum</i>	<i>Cornus amomum</i>	<i>Juncus effusus</i>
<i>Apocynum cannabinum</i>	<i>Crataegus</i> sp.	<i>Juniperus communis</i>
<i>Aquilegia canadensis</i>	<i>Cyperus strigosus</i>	<i>Juniperus virginiana</i>
<i>Asclepias tuberosa</i>	<i>Dactylis glomerata</i>	<i>Larix laricina</i>
<i>Aster laevis</i>	<i>Desmodium canadense</i>	<i>Lobelia inflata</i>
<i>Aster pilosus</i> var. <i>pilosus</i>	<i>Dipsacus fullonum</i>	<i>Lobelia kalmii</i>
<i>Aster prenanthoides</i>	<i>Drosera rotundifolia</i>	<i>Lobelia siphilitica</i>
<i>Aster puniceus</i>	<i>Eleagnus umbellatus</i>	<i>Lonicera tatarica</i>
<i>Aster umbellatus</i>	<i>Epilobium ciliatum</i>	<i>Lycopus americanus</i>
<i>Betula lutea</i>	<i>Equisetum hymale</i>	<i>Lysimachia nummularia</i>
<i>Betula papyrifera</i>	<i>Equisetum variegatum</i>	<i>Malus pumila</i>
<i>Bidens tripartita</i>	<i>Erigeron annuus</i>	<i>Medicago lupulina</i>
<i>Carex aurea</i>	<i>Erigeron strigosus</i>	<i>Melilotus altissima</i>
<i>Carex flava</i>	<i>Eupatorium maculatum</i>	<i>Melilotus officinalis</i>

APPENDIX II (continued)

In 5-25% of sites (continued)

<i>Mentha arvensis</i>	<i>Prunus virginiana</i>	<i>Thelypteris palustris</i>
<i>Muhlenbergia mexicana</i>	<i>Quercus macrocarpa</i>	<i>Thuja occidentalis</i>
<i>Myrica pensylvanica</i>	<i>Quercus rubra</i>	<i>Tilia americana</i>
<i>Oenothera biennis</i>	<i>Rhamnus cathartica</i>	<i>Toxicodendron radicans</i>
<i>Oenothera perennis</i>	<i>Robinia pseudo-acacia</i>	<i>Tussilago farfara</i>
<i>Onoclea sensibilis</i>	<i>Rosa sp.</i>	<i>Typha angustifolia</i>
<i>Ostrya virginiana</i>	<i>Salix humilis</i>	<i>Typha sp.</i>
<i>Parnassia glauca</i>	<i>Salix petiolaris</i>	<i>Ulmus americana</i>
<i>Pastinaca sativa</i>	<i>Salix rigida</i>	<i>Ulmus thomasii</i>
<i>Pedicularis lanceolata</i>	<i>Schizachyrium scoparium</i>	<i>Valeriana officinalis</i>
<i>Penstemon digitalis</i>	<i>Scirpus cyperinus</i>	<i>Verbena hastata</i>
<i>Poa compressa</i>	<i>Senecio aureus</i>	<i>Veronica arvensis</i>
<i>Populus deltoides</i>	<i>Shepherdia canadensis</i>	<i>Veronica officinalis</i>
<i>Populus grandidentata</i>	<i>Sisyrinchium sp.</i>	<i>Vicia cracca</i>
<i>Potentilla fruticosa</i>	<i>Solidago rugosa</i>	<i>Vitis sp.</i>
<i>Potentilla recta</i>	<i>Spiranthes romanzoffiana</i>	

In < 5% of sites

<i>Ailanthus altissima</i>	<i>Erigeron pulchellus</i>	<i>Prunus serotina</i>
<i>Amelanchier (arborea)</i>	<i>Euphrasia randii</i>	<i>Pyrus communis</i>
<i>Anaphalis margaritacea</i>	<i>Euphrasia strictum</i>	<i>Quercus muhlenbergii</i>
<i>Andropogon gerardii</i>	<i>Fagus grandifolia</i>	<i>Rhus aromatica</i>
<i>Anemone cylindrica</i>	<i>Festuca rubra</i>	<i>Rhus typhina</i>
<i>Angelica atropurpurea</i>	<i>Galium pilosum</i>	<i>Ribes cynos-bati</i>
<i>Apocynum (androsaemifolium)</i>	<i>Galium triflorum</i>	<i>Rubus flagellaris</i>
<i>Aster cordifolius</i>	<i>Gentiana andrewsii</i>	<i>Rubus idaeus</i>
<i>Aster ericoides</i>	<i>Gentiana clausa</i>	<i>Rubus odoratus</i>
<i>Aster undulatus</i>	<i>Gentianella quinquefolia</i>	<i>Salix nigra</i>
<i>Berberis thunbergii</i>	<i>Geranium maculatum</i>	<i>Salix purpurea</i>
<i>Bidens frondosa</i>	<i>Glechoma hederacea</i>	<i>Scirpus pendulus</i>
<i>Bromus kalmii</i>	<i>Hamamelis virginiana</i>	<i>Setaria glauca</i>
<i>Bromus tectorum</i>	<i>Iris pseudacorus</i>	<i>Solidago bicolor</i>
<i>Calamagrostis sp.</i>	<i>Juncus alpinus</i>	<i>Solidago patula</i>
<i>Carex complanata</i>	<i>Juncus brachycephalus</i>	<i>Sorbus americana</i>
<i>Carex folliculata</i>	<i>Juncus torreyi</i>	<i>Sorghastrum nutans</i>
<i>Carex granularis</i>	<i>Lilium philadelphicum</i>	<i>Spiranthes cernua</i>
<i>Carex gynandra</i>	<i>Liriodendron tulipifera</i>	<i>Spirea alba</i>
<i>Carex normalis</i>	<i>Lonicera dioica</i>	<i>Spirea tomentosa</i>
<i>Carex tribuloides</i>	<i>Lonicera (tatarica/morrowi)</i>	<i>Thalictrum dioicum</i>
<i>Celastrus scandens</i>	<i>Lysimachia ciliata</i>	<i>Thalictrum pubescens</i>
<i>Centaurea maculosa</i>	<i>Malva moschata</i>	<i>Tridens flavus</i>
<i>Cirsium arvense</i>	<i>Monarda didyma</i>	<i>Trifolium aureum</i>
<i>Cirsium pumilum</i>	<i>Monarda fistulosa</i>	<i>Trifolium hybridum</i>
<i>Cirsium vulgare</i>	<i>Muhlenbergia glomerata</i>	<i>Ulmus rubra</i>
<i>Cynachum nigrum</i>	<i>Myosotis scorpioides</i>	<i>Vaccinium angustifolium</i>
<i>Danthonia compressa</i>	<i>Oenothera cruciata</i>	<i>Vaccinium corymbosum</i>
<i>Desmodium paniculatum</i>	<i>Origanum vulgare</i>	<i>Veronica chamaedrys</i>
<i>Dianthus armeria</i>	<i>Oxalis stricta</i>	<i>Viburnum lentago</i>
<i>Eleocharis palustris</i>	<i>Phalaris arundinacea</i>	<i>Viburnum opulus</i>

Epilobium ciliatum
 subsp. *glandulosum*
Epilobium leptophyllum
Erigeron philadelphicus

Picea mariana
Platanus occidentalis
Populus balsamifera

Viburnum rafinesquianum
Vitis riparia
Zanthoxylum americanum

REFERENCES

- ABBEY, F. M. (1930). Habits of the fringed gentian. *Horticulture*, **8**, 49.
- AHMADJIAN, V. (1979). *Flowering Plants of Massachusetts*. University of Massachusetts Press, Amherst, Massachusetts.
- ALLEN, S. E., GRIMSHAW, H. M., PARKINSON, J. A. & QUARMBY, C. (1974). Analysis of soils. *Chemical Analysis of Ecological Materials* (Ed by S. E. Allen), pp. 13-68. John Wiley & Sons, New York.
- ANDREAS, B. K. & COOPERRIDER, T. S. (1981) The Gentianaceae and Menyanthaceae of Ohio. *Castanea*, **146**, 102-108.
- AUSTIN, M. P. & AUSTIN, B. O. (1980). Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68**, 891-918.
- BALDWIN, W. K. W. (1958) *Plants of the Clay Belt of Northern Ontario and Quebec*. National Museum of Canada, Ottawa. Bulletin No. 156.
- BARBOUR, M. G. & BILLINGS, W. D. (1988). *North American Terrestrial Vegetation*. Cambridge University Press, Cambridge.
- BARD, G. E. (1952). Secondary succession on the Piedmont of New Jersey. *Ecological Monographs*, **22**, 195-216.
- BASKIN, J. M. & BASKIN, C. C. (1979). Studies on the autecology and population biology of the monocarpic perennial *Grindelia lanceolata*. *American Midland Naturalist*, **41**, 290-299.
- BASKIN, J. M., BRYAN, H. D. & BASKIN, C. C. (1986). Ecological life cycle of *Synandra hispidula* in northcentral Kentucky. *Bulletin of the Torrey Botanical Club*, **113**, 168-172.
- BATTY, P. M., BATTY, B. D. & MILLER, G. R. (1984). Population size and reproduction of *Gentiana nivalis* L. at Ben Lawers N. N. R. *Transactions of the Botanical Society of Edinburgh*, **44**, 269-280.
- BEGON, M. (1985). A general theory of life history variation. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour, 25th Symposium of the British Ecological Society* (Ed by R. M. Sibly & R. H. Smith), pp. 91-97. Blackwell Scientific Publications, Oxford.
- BIRSE, E. L. (1982). Plant communities on serpentine in Scotland. *Vegetatio*, **49**, 141-162.
- BLACKMAN, G. E. & RUTTER, A. J. (1954). *Endymion non-scriptus*: Biological Flora of the British Isles. *Journal of Ecology*, **42**, 629-638.
- BLYTH, C. R. & STILL, H. A. (1983). Binomial confidence intervals. *Journal of the American Statistical Association*, **78**, 108-116.
- BOHLEN, C. C. (1990). *The Control of Plant Species Diversity in Cattail-dominated Wetlands in Central New York*. Ph.D. thesis, Cornell University, Ithaca, New York.
- BOYER, M. L. H. & WHEELER, B. D. (1989). Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. *Journal of Ecology*, **77**, 597-609.
- BRADSHAW, A. D. (1987). Comparison - its scope and limits. *New Phytologist*, **106**, 3-21.

- BRAUN, E. L. (1950). *Deciduous Forests in Eastern North America*. Blakiston Co., Philadelphia (reprinted 1964, Hafner, New York).
- BRITTON, E. G. (1916). Wild plants needing protection: 12. "Fringed Gentian" (*Gentiana crinita* Froel.). *Journal of the New York Botanical Garden*, **17**, 81-82.
- BRITTON, E. G. (1923). Cultivation of the Fringed Gentian. *Journal of the New York Botanical Garden*, **24**, 258-259.
- BRITTON, E. G. (1924). The fringed gentian - *Gentiana crinita* Froel. *Torrey*, **24**, 102-103.
- BRITTON, E. G. (1925). *Gentiana crinita*. *Journal of the New York Botanical Garden*, **26**, 40-41.
- BROWN, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255-279.
- BRUCE, H. (1976). *How to Grow Wildflowers and Trees in Your Own Garden*. Alfred A. Knopf, New York.
- BURGMAN, M. A. (1989). The habitat volumes of scarce and ubiquitous plants: a test of the model of environmental control. *American Naturalist*, **133**, 228-239.
- BYER, M. D. (1969). The role of physical environment in some tracheophyte distributions along a soil moisture gradient. *Bulletin of the Torrey Botanical Club*, **96**, 191-201.
- CARLQUIST, S. (1967). The biota of long-distance dispersal, V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club*, **94**, 129-162.
- CHEW, F. S. & COURTNEY, S. P. (1991). Plant apparency and evolutionary escape from insect herbivory. *American Naturalist*, **138**, 729-750.
- CHEW, V. (1977). *Comparisons Among Treatment Means in an Analysis of Variance*. United States Department of Agriculture, Agricultural Research Service, Washington, D. C.
- CLAPHAM, A. R., TUTIN, T. G. & MOORE, D. M. (1987). *Flora of the British Isles*, 3rd edn. Cambridge University Press, Cambridge.
- CLINE, M. G. (1955). *Soils and Soil Associations of New York*. New York State College of Agriculture, Cornell University, Ithaca, New York. Cornell Extension Bulletin 930.
- CONOVER, W. J. (1980). *Practical Non-Parametric Statistics*, 2nd edn. John Wiley & Sons, New York.
- COOK, R. E. (1980). The biology of seeds in the soil. *Demography and Evolution in Plant Populations* (Ed by O. T. Solbrig), pp. 107-129. Botanical Monographs, Volume 15. University of California Press, Berkeley.
- CORNELL COOPERATIVE EXTENSION (1990). *1990 Cornell Recommends for Field Crops*. Cornell University, Ithaca, New York.
- CRAWLEY, M. J. (1988). Herbivores and plant population dynamics. *Plant Population Ecology: 28th Symposium of the British Ecological Society* (Ed by A. J. Davy, M. J. Hutchings & A. R. Watkinson), pp. 367-392. Blackwell Scientific Publications, Oxford.

- CRAWLEY, M. J. & NACHAPONG, M. (1985). The establishment of seedlings from primary and regrowth seeds of ragwort (*Senecio jacobea*). *Journal of Ecology*, **73**, 255-261.
- DALE, H. M. (1974). The biology of Canadian weeds, 5. *Daucus carota*. *Canadian Journal of Plant Science*, **54**, 673-685.
- DALE, H. M. & HARRISON, P. J. (1966). Wild carrot seeds: germination and dormancy. *Weed Science*, **14**, 201-204.
- DAVIS, M. B. (1983). Holocene vegetational history of the eastern United States. *Late-Quaternary Environments of the United States*, vol. 2 (Ed by H. E. Wright, Jr.), pp. 166-181. University of Minnesota Press, Minneapolis.
- DAVIS, R. B. & JACOBSON, G. L., JR. (1985). Late-glacial and early Holocene landscapes in northern New England and adjacent areas of Canada. *Quaternary Research*, **23**, 341-368.
- DE JONG, T. J. & KLINKHAMER, P. G. L. (1988). Population ecology of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a coastal sand dune area. *Journal of Ecology*, **76**, 366-382.
- DE JONG, T. J., KLINKHAMER, P. G. L. & METZ, J. A. J. (1987). Selection for biennial life histories. *Vegetatio*, **70**, 149-156.
- DEAM, C. C. (1940). *Flora of Indiana*. Indiana Department of Conservation, Indianapolis, Indiana.
- DEMUTH, K., FORSTREUTER, W. & WEBER, H. C. (1991). Morphological differences in vesicular-arbuscular mycorrhizae of Gentianaceae produced by different endophytes. *Flora: Morphologie, Geobotanik, Ökologie*, **185**, 127-132.
- DORE, W. G. & GILLETT, J. M. (1955) *Botanical Survey of the St. Lawrence Seaway Area in Ontario*. Department of Agriculture, Ottawa.
- DRURY, W. H. (1980). Rare species of plants. *Rhodora*, **82**, 3-48.
- DURING, H. J., SCHENKEVELD, A. J., VERKAAR, H. J. & WILLENS, J. H. (Eds.) (1985). Demography of short-lived forbs in chalk grassland in relation to vegetation structure. *The Population Structure of Vegetation* (Ed by J. White), pp. 341-370. Dr. W. Junk, Publishers, Dordrecht.
- EASTERLY, N. W. (1979). Rare and infrequent plant species in the oak openings of northwestern Ohio. *Ohio Journal of Science*, **79**, 51-58.
- ETHERINGTON, J. R. (1982). *Environment and Plant Ecology*, 2nd edn. John Wiley & Sons, New York.
- FARMER, R. E., JR. (1978). Propagation of a southern Appalachian population of fringed gentians. *Bulletin of the Torrey Botanical Club*, **105**, 139-142.
- FENNER, M. (1978). A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *Journal of Ecology*, **66**, 953-963.
- FENNER, M. (1985). *Seed Ecology*. Chapman and Hall Ltd., London.
- FERNALD, M. L. (1950). *Gray's Manual of Botany*, 8th edn. Van Nostrand Reinhold Company, New York.

- FULLARD, H., DARBY, H. C., WILLETT, B. M. & GAYLORD, D. (1981). *The library atlas, 15th edn.* George Philip, London.
- FUTUYMA, R. P. (1990). Paleoecology of a marl fen: Byron-Bergen Swamp, Genesee County, New York. *New York Natural History Conference, Albany, June 20-22, 1990; Program and Abstracts. New York State Museum Circular*, **54**, p. 30.
- GAY, P. E., GRUBB, P. J. & HUDSON, H. J. (1982). Seasonal changes in the concentrations of nitrogen, phosphorus and potassium and in the density of mycorrhiza in biennial and matrix-forming perennial species of closed chalkland turf. *Journal of Ecology*, **70**, 571-593.
- GEHLBACH, F. R. & POLLEY, H. W. (1982). Relict trout lilies *Erythronium mesochoreum* in central Texas: a multivariate analysis of habitat for conservation. *Biological Conservation*, **22**, 251-258.
- GHOSAL, S. & JAISWAL, D. K. (1980). Chemical constituents of Gentianaceae, XXVIII: Flavonoids of *Enicostemma hyssopifolium* (Willd.) Verd. *Journal of Pharmaceutical Sciences*, **69**, 53-56.
- GIERSBACH, J. (1937). Some factors affecting germination and growth of gentian. *Contributions from the Boyce Thompson Institute*, **19**, 91-103.
- GILLET, J. M. (1957). A revision of the North American species of *Gentianella* Moench. *Annals of the Missouri Botanical Garden*, **44**, 195-270.
- GILLET, J. M. (1963). The gentians of Canada, Alaska and Greenland. *Canada Department of Agriculture, Publication* **1180**, 1-99.
- GLEASON, H. A. (1952). *The New Britton and Brown Illustrated Flora of the Northeastern United States and Adjacent Canada.* Hafner Press, Macmillan Publishing Company, New York.
- GODWIN, H. (1975). *History of the British Flora: A Factual Basis for Phytogeography, 2nd edn.* Cambridge University Press, Cambridge.
- GOLDBERG, D. E. (1987). Seedling colonization of experimental gaps in two old-field communities. *Bulletin of the Torrey Botanical Club*, **114**, 139-148.
- GOLDBERG, D. E. & GROSS, K. L. (1988). Disturbance regimes of mid-successional old-fields. *Ecology*, **69**, 1677-1688.
- GOODWIN, R. H. (1943). The flora of Mendon Ponds Park. *Proceedings of the Rochester Academy of Science*, **8**, 233-245.
- GORMAN, M. (1979). *Island Ecology.* Chapman and Hall Ltd., London.
- GRAVES, C. B., EAMES, E. H., BISSELL, C. H., ANDREWS, L., HARGER, E. B. & WEATHERBY, C. A. (1910) *Catalogue of the Flowering Plants and Ferns of Connecticut Growing without Cultivation.* Connecticut State Geological and Natural History Survey, Hartford, Connecticut. Bulletin No. 14.
- GREEN, J. (1814). *An Address on the Botany of the United States, Delivered Before the Society for the Promotion of Useful Arts; to which is Added a Catalogue of Plants Indigenous to the State of New York.* Printed by Webster & Skinners, Albany, New York.
- GREENSLADE, P. J. M. (1983). Adversity selection and the habitat templet. *American Naturalist*, **122**, 352-365.

- GREIG-SMITH, J. & SAGAR, J. R. (1981). Biological causes of local rarity in *Carlina vulgaris*. *The Biological Aspects of Rare Plant Conservation* (Ed by H. Synge), pp. 390-400. John Wiley & Sons, New York.
- GRIGGS, R. F. (1940). The ecology of rare plants. *Bulletin of the Torrey Botanical Club*, **67**, 565-594.
- GRIME, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169-1194.
- GRIME, J. P., HODGSON, J. G. & HUNT, R. (1988). *Comparative Plant Ecology*. Unwin Hyman, London.
- GROSS, K. L. (1980). Colonization by *Verbascum thapsus* (Mullein) of an old field in Michigan: experiments on the effects of vegetation. *Journal of Ecology*, **68**, 919-927.
- GROSS, K. L. (1981). Predictions of fate from rosette size in four "biennial" plant species, *Verbascum thapsus*, *Oenothera biennis*, *Daucus carota*, and *Tragopogon dubius*. *Oecologia*, **48**, 209-213.
- GROSS, K. L. (1984). Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology*, **72**, 369-387.
- GROSS, K. L. & WERNER, P. A. (1982). Colonizing abilities of "biennial" plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology*, **63**, 921-931.
- GRUBB, P. J. (1976). A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland system. *Biological Conservation*, **10**, 53-76.
- GRUBB, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review*, **52**, 107-145.
- GRUBB, P. J. (1986). Problems posed by sparse and patchily distributed species in species-rich plant communities. *Community Ecology* (Ed. by J. Diamond and T. J. Case), Chapter 12, pp. 207-255. Harper & Row, New York.
- GRUBB, P. J. (1989). Toward a more exact ecology: a personal view of the issues. *Toward a More Exact Ecology, 30th Symposium of the British Ecological Society* (Ed by P. J. Grubb & J. B. Whittaker), pp. 3-29. Blackwell Scientific Publications, Oxford.
- GRUBB, P. J., KELLY, D. & MITCHLEY, J. (1982). The control of relative abundance in communities of herbaceous plants. *The Plant Community as a Working Mechanism* (Ed by E. I. Newman), pp. 79-97. Blackwell Scientific Publications, Oxford.
- HACKETT, C. (1965). Ecological aspects of the nutrition of *Deschampsia flexuosa* (L.) Trin.: II. The effects of aluminium, calcium, iron, potassium, manganese, phosphorus and pH on the growth of seedlings and established plants. *Journal of Ecology*, **53**, 315-333.
- HALL, J. (1843). *Geology of New York, Part IV: Comprising the Survey of the Fourth Geological District*. Carroll & Cook, Printers to the Assembly, Albany, New York.
- HANSEN, A. A. (1923). Fringed gentian (*Gentiana crinita*). *Nature Magazine*, **2**, 357-358, 363.
- HARPER, J. L. (1977). *Population Biology of Plants*. Academic Press, London.

- HARPER, J. L. (1981). The meanings of rarity. *The Biological Aspects of Rare Plant Conservation* (Ed by H. Synge), pp. 189-203. John Wiley & Sons, New York.
- HART, R. (1977). Why are biennials so few? *American Naturalist*, **111**, 792-799.
- HARVEY, H. J. (1985). Population biology and the conservation of rare species. *Studies on Plant Demography: A Festschrift for John L. Harper* (Ed by J. White), pp. 111-123. Academic Press, New York.
- HEDDEN, E. N. (1931). Pot-grown gentians from seed. *Horticulture* **9**, 80.
- HENDRIX, S. D. (1979). Compensatory reproduction in a biennial herb following insect defloration. *Oecologia*, **42**, 107-118.
- HODGSON, J. G. (1986a). Commonness and rarity in plants with special reference to the Sheffield flora: Part I. The identity and habitat characteristics of the common and rare species. *Biological Conservation*, **36**, 199-252.
- HODGSON, J. G. (1986b). Commonness and rarity in plants with special reference to the Sheffield flora: Part III. Taxonomic and evolutionary aspects. *Biological Conservation*, **36**, 275-296.
- HOLT, B. R. (1972). Effect of arrival time on recruitment, mortality and reproduction in successional plant populations. *Ecology*, **53**, 668-673.
- HUISKES, AD. H. L. & STEINSTR, A. W. (1985). Disasters and catastrophes in populations of *Halimione portulacoides*. *Studies in Plant Demography: A Festschrift for John L. Harper* (Ed. by J. White), Chapter 6, pp. 83-93.
- ILTIS, H. H. (1965). The genus *Gentianopsis* (Gentianaceae): Transfers and phytogeographic comments. *SIDA*, **2**, 129-154.
- JACQUELINET-JEANMOUGIN, S. & GIANINAZZI-PEARSON, V. (1983). Endomycorrhizas in the Gentianaceae, I. The fungi associated with *Gentiana lutea* L. *New Phytologist*, **95**, 663-666.
- JOHNSON, C. D. & THOMAS, A. G. (1978). Recruitment and survival of seedlings of a perennial *Hieracium* species in a patchy environment. *Canadian Journal of Botany*, **56**, 572-580.
- JOHNSTON, C. A. & NAIMAN, R. J. (1990). Aquatic patch reation in relation to beaver population trends. *Ecology*, **71**, 1617-1621.
- JONES, G. N. (1963a) *Flora of Illinois, 3rd edn*. University of Notre Dame Press, Notre Dame, Indiana.
- JONES, W. H. S. (1963b). *English Translation of Pliny's Natural History*. Harvard University Press, Cambridge, Massachusetts.
- KARLSONN, T. (1974). Recurrent ecotypic variation in Rhinanthaeae and Gentianaceae in relation to hemiparasitism and mycotrophy. *Botaniska Notiser*, **127**, 527-539.
- KEIZER, P. J., VAN TOOREN, B. F. & DURING, H. J. (1985). Effects of bryophytes on seedling emergence and establishment of short-lived forbs in chalk grassland. *Journal of Ecology*, **73**, 493-504.

- KELLY, D. (1984). Seeds per fruit as a function of fruits per plant in depauperate annuals and biennials. *New Phytologist*, **96**, 103-114.
- KELLY, D. (1985). On strict and facultative biennials. *Oecologia*, **67**, 292-294.
- KELLY, D. (1989a). Demography of short-lived plants in chalk grassland, I. Life cycle variation in annuals and strict biennials. *Journal of Ecology*, **77**, 747-769.
- KELLY, D. (1989b). Demography of short-lived plants in chalk grassland, II. Control of mortality and fecundity. *Journal of Ecology*, **77**, 770-784.
- KELLY, D. (1989c). Demography of short-lived plants in chalk grassland, III. Population stability. *Journal of Ecology*, **77**, 785-798.
- KLEMOW, K. M. & RAYNAL, D. J. (1985). Demography of two facultative biennial plant species in an unproductive habitat. *Journal of Ecology*, **73**, 147-167.
- KLINKHAMER, P. G. L. & DE JONG, T. J. (1983). Is it profitable for biennials to live longer than two years? *Ecological Modelling*, **20**, 223-232.
- KNAPP, W. W. & EGGLESTON, K. L. (1989). *An Analysis of the Drought in the Northeast: The Climatic Conditions and their Impacts*. Northeast Regional Climate Center, Cornell University, Ithaca, New York.
- KNIPE, P. R. (1988). *Gentianella ciliata* (L.) Borkh. in Buckinghamshire. *Watsonia*, **17**, 94-95.
- KRUCKEBERG, A. R. & RABINOWITZ, D. (1985). Biological aspects of endemism in higher plants. *Annual Review of Ecology & Systematics*, **16**, 447-479.
- LACEY, E. P. (1978). *The Phenology of Seed Dispersal in Daucus carota L. ssp. carota (Apiaceae): An Ecological and Evolutionary Study*. Ph. D. thesis, University of Michigan, Ann Arbor, Michigan.
- LACEY, E. P. (1980). The influence of hygroscopic movement on seed dispersal in *Daucus carota* (Apiaceae). *Oecologia (Berlin)*, **47**, 110-114.
- LACEY, E. P. (1982). The timing of seed dispersal in *Daucus carota*. *Oikos*, **39**, 83-91.
- LACEY, E. P. (1986). The genetic and environmental control of reproductive timing in a short-lived monocarpic species *Daucus carota* (Umbelliferae). *Journal of Ecology*, **74**, 73-86.
- LANDA, K. & RABINOWITZ, D. (1983). Relative preference of *Arphia sulphurea* (Orthoptera: Acrididae) for sparse and common prairie grasses. *Ecology*, **64**, 392-395.
- LOUDA, S. M. (1982). Limitation of recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. *Journal of Ecology*, **70**, 43-53.
- LOUDA, S. M. (1983). Seed predation and seedling mortality in the recruitment of a shrub, *Haplopappus venetus* (Asteraceae) along a climatic gradient. *Ecology*, **64**, 511-521.
- LOUDA, S. M. (1984). Herbivore effect on stature, fruiting, and leaf dynamics of a native crucifer. *Ecology*, **65**, 1379-1386.

- MACDONALD, H. (1977) *Native Manitoba Plants in Bog, Bush, and Prairie*. Manitoba Department of Agriculture, Winnipeg.
- MARKS, P. L. (1983). On the origin of the field plants of the northeastern United States. *American Naturalist*, **122**, 210-228.
- MARKS, P. L. & GARDESCU, S. (1992). Vegetation of the central Finger Lakes region of New York in the 1790s. *Late Eighteenth Century Vegetation of Central and Western New York State on the Basis of Original Land Surveys*, pp. 1-35. *New York State Museum Bulletin*, No. **484**.
- MASCHINSKI, J. & WHITHAM, T. G. (1989). The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist*, **134**, 1-19.
- MATSHAT, C. H. (1933). Raising fringed gentians from seed. *Gardener's Chronicle of America*, **37**, 279-280.
- MENGES, E. S. (1988). *Conservation Biology of Furbish's Lousewort: Final Report to Region 5, U. S. Fish and Wildlife Service*. Butler University, Indianapolis, Indiana. Holcomb Research Institute Report No. 126.
- MILES, J. (1974). Effects of experimental interference with stand structure on establishment of seedlings in Callunetum. *Journal of Ecology*, **62**, 675-687.
- MILLER, N. G. (1973). Late-glacial plants and plant communities in northwestern New York State. *Journal of the Arnold Arboretum*, **54**, 123-159.
- MILLER, N. G. (1989). Pleistocene and Holocene floras of New England as a framework for interpreting aspects of plant rarity. *Rhodora*, **91**, 49-69.
- MILLER, N. G. (1990). The management of rare plants: suggestions derived from paleoecological studies of Late-Pleistocene floras. *Ecosystem Management: Rare Species and Significant Habitats; Proceedings of the 15th Annual Natural Areas Conference* (Ed by R. S. Mitchell, C. J. Sheviak & D. J. Leopold), pp. 159-162. The New York State Education Department, Albany, New York. *New York State Museum Bulletin* No. **471**.
- MITCHELL, R. S. (1986). *A Checklist of New York State Plants*. The New York State Education Department, Albany, New York. *New York State Museum Bulletin* No. **458**.
- MITCHLEY, J. & GRUBB, P. J. (1986). Control of relative abundance of perennials in chalk grassland in southern England: I. Constancy of rank order and results of pot and field experiments on the role of interference. *Journal of Ecology*, **74**, 1139-1166.
- MOHLENBROCK, R. H. (1986) *Guide to the Vascular Flora of Illinois*. Southern Illinois University Press, Carbondale, Illinois.
- MOLONEY, K. A. (1990). Shifting demographic control of a perennial bunchgrass along a natural habitat gradient. *Ecology*, **71**, 1133-1143.
- MORGAN, L. H. (1868, reprinted 1986). *The American Beaver*. Dover Publications, Inc., New York.
- MUENSCHER, W. C. (1946). The vegetation of Bergen Swamp: I. The vascular plants. *Proceedings of the Rochester Academy of Science*, **9**, 64-117.

- MULLER, E. H., BRAUN, D. D., YOUNG, R. A. & WILSON, M. P. (1988). Morphogenesis of the Genesee Valley. *Northeastern Geology*, **10**, 112-133.
- MURPHY, G. I. (1968). Pattern in life history and the environment. *American Naturalist*, **102**, 391-403.
- NAIMAN, R. J., MELILLO, J. M. & HOBIE, J. E. (1986). Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology*, **67**, 1254-1269.
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA) (1987-1989). *Climatological Data, New York, vols. 99-101*. Environmental Data Service, U. S. Department of Commerce/National Environmental Satellite, Data, and Information Service, National Climatic Data Center, Asheville, North Carolina.
- NATURE CONSERVANCY COUNCIL (1989). *Guidelines for Selection of Biological SSSIs*. Nature Conservancy Council, Peterborough, England.
- NEARING, G. G. (1932). Experimenting with fringed gentians. *Horticulture*, **10**, 313.
- NORTON, G. F. (1923). How to have Fringed Gentians. *Journal of the New York Botanical Garden*, **24**, 256-258.
- NORTON, G. F. (1925). The fringed gentian. *Journal of the New York Botanical Garden*, **26**, 38-40.
- OKUBO, A. & LEVIN, S. A. (1989). A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329-338.
- OOSTING, H. J. & HUMPHREYS, M. E. (1940). Buried viable seeds in a successional series of old field and forest soils. *Bulletin of the Torrey Botanical Club*, **67**, 253-273.
- OSTMAN, N. & MARKS, P. L. (1990). *An Evaluation of Cornell's Natural Areas*. Cornell Plantations Unpublished Report, Cornell University, Ithaca, New York.
- PAIGE, K. N. & WHITHAM, T. G. (1987). Overcompensation in response to mammalian herbivory: the advantage of being eaten. *American Naturalist*, **129**, 407-416.
- PAINE, J. A., JR. (1865). *Catalogue of Plants Found in Oneida County and Vicinity*. Report of the Regents of the University of the State of New York, C. Wendell, Printer, Albany, New York.
- PARKER, M. A. & ROOT, R. B. (1981). Insect herbivores limit habitat distribution of a native composite *Machaeranthera canescens*. *Ecology*, **62**, 1390-1392.
- PERRING, F. H. & FARRELL, L. (1983). *British Red Data Books: 1. Vascular Plants, 2nd edn*. Royal Society for Nature Conservation, Lincoln, England.
- PICKETT, S. T. A. (1982). Population patterns through twenty years of oldfield succession. *Vegetatio*, **49**, 45-59.
- PICKETT, S. T. A. & BAZZAZ, F. A. (1978). Organization of an assemblage of early successional species on a soil moisture gradient. *Ecology*, **59**, 1248-1255.
- PIGOTT, C. D. & WALTERS, S. M. (1954). On the interpretation of the discontinuous distributions shown by certain British species of open habitats. *Journal of Ecology*, **42**, 95-116.

- PULLIAM, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- RABINOWITZ, D. (1978a). Abundance and diaspore weight in rare and common prairie grasses. *Oecologia*, **37**, 213-219.
- RABINOWITZ, D. (1978b). Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. *Journal of Biogeography*, **5**, 113-133.
- RABINOWITZ, D. (1981). Seven forms of rarity. *The Biological Aspects of Rare Plant Conservation* (Ed by H. Synge), pp. 205-217. John Wiley & Sons, New York.
- RABINOWITZ, D., CAIRNS, S. & DILLON, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. *Conservation Biology: The Science of Scarcity and Diversity* (Ed. by M. E. Soulé), pp. 182-204. Sinauer Associates, Sunderland, Massachusetts.
- RABINOWITZ, D. & RAPP, J. K. (1979). Dual dispersal modes in hairgrass, *Agrostis hiemalis* (Walt.) B. S. P. (Gramineae). *Bulletin of the Torrey Botanical Club*, **106**, 32-36.
- RABINOWITZ, D. & RAPP, J. K. (1985). Colonization and establishment of Missouri prairie plants on artificial soil disturbances: III. Species abundances, distributions, survivorship, and rarity. *American Journal of Botany*, **72**, 1635-1640.
- RABINOWITZ, D., RAPP, J. K., CAIRNS, S. & MAYER, M. (1989). The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. *American Naturalist*, **134**, 525-544.
- RABINOWITZ, D., RAPP, J. K. & DIXON, P. M. (1984). Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology*, **65**, 1144-1154.
- REED, C. F. (1986). *Floras of Serpentine Formations in Eastern North America: with Descriptions of Geomorphology and Mineralogy of the Formations*. Reed Herbarium, Baltimore, Maryland.
- REINARTZ, J. A. (1984). Life history variation of common mullein (*Verbascum thapsus*): I. Latitudinal differences in population dynamics and timing of reproduction. *Journal of Ecology*, **72**, 897-912.
- ROBERTS, H. A. (1986). Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology*, **23**, 639-656.
- ROBERTS, H. A. & FEAST, P. M. (1972). Fate of seeds of some annual weeds in different depths of cultivated and undisturbed soil. *Weed Research*, **12**, 316-324.
- RORISON, I. H. (1960a). Some experimental aspects of the calcicole-calcifuge problem: I. The effects of competition and mineral nutrition upon seedling growth in the field. *Journal of Ecology*, **48**, 585-599.
- RORISON, I. H. (1960b). Some experimental aspects of the calcicole-calcifuge problem: II. The effects of mineral nutrition on seedling growth in solution culture. *Journal of Ecology*, **48**, 679-688.
- SALISBURY, E. J. (1942). *The Reproductive Capacity of Plants; Studies in Quantitative Biology*. G. Bell & Sons Ltd., London.
- SANDERS, J. (1986). Treasures among the wildflowers. *The New York Times*, Sunday, September 21, p. 35.

SAS INSTITUTE INC. (1985). *SAS® User's Guide: Statistics, Version 5 Edition*. SAS Institute Inc., Cary, North Carolina.

SCHENKEVELD, A. J. & VERKAAR, H. J. (1984). The ecology of short-lived forbs in chalk grasslands: distribution of germinative seeds and its significance for seedling emergence. *Journal of Biogeography*, **11**, 251-260.

SCHMIDT, W. (1989). Plant dispersal by motor cars. *Vegetatio*, **80**, 147-152.

SCHUSTER, R. M. (1949). The ecology and distribution of Hepaticae in central and western New York. *The American Midland Naturalist*, **42**, 513-712.

SCOGGAN, H. J. (1957) *Flora of Manitoba*. National Museum of Canada. Bulletin No. 140.

SEISCHAB, F. K. (1990). Presettlement forests in the Phelps and Gorham Purchase in western New York. *Bulletin of the Torrey Botanical Club*, **117**, 27-38.

SEMPERS, J. F. (1904). The young fringed gentian. *The American Botanist*, **6**, 2-4.

SEMPERS, J. F. (1905a). Fringed gentian notes. *The American Botanist*, **7**, 91-93.

SEMPERS, J. F. (1905b). Fringed gentian notes. *The American Botanist*, **8**, 30-32.

SEVERINGHAUS, C. W. & BROWN, C. P. (1956). History of white-tailed deer in New York. *New York Fish and Game Journal*, **3**, 129-167.

SEVERINGHAUS, C. W. & BROWN, C. P. (1970). Deer take 1956-1970. *Unpublished leaflet*. [from R. Gotie, Department of Environmental Conservation, Cortland, New York].

SEYMOUR, F. C. (1982) *The Flora of New England, 2nd edn*. Phytologia Memoirs V, H. N. Moldenke and A. L. Moldenke (publishers), Plainfield, New Jersey.

SHAFFER, M. L. (1981). Minimum population sizes for species conservation. *Bioscience*, **31**, 131-134.

SHANKS, R. E. (1966). An ecological survey of the vegetation of Monroe County, New York. *Proceedings of the Rochester Academy of Science*, **11**, 108-252.

SHARITZ, R. & MCCORMICK, J. (1973). Population dynamics of two competing annual plant species. *Ecology*, **54**, 723-740.

SHMIDA, A. & ELLNER, S. P. (1984). Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29-55.

SILVERTOWN, J. W. (1980). Leaf-canopy-induced seed dormancy in a grassland flora. *New Phytologist*, **85**, 109-118.

SILVERTOWN, J. W. (1981). Micro-spatial heterogeneity and seedling demography in species-rich grassland. *New Phytologist*, **88**, 117-128.

SILVERTOWN, J. W. (1983). Why are biennials sometimes not so few? *American Naturalist*, **121**, 448-453.

SILVERTOWN, J. W. (1984). Death of the elusive biennial. *Nature*, **310**, 271.

- SILVERTOWN, J. W. (1986). "Biennials": a reply to Kelly. *American Naturalist*, **127**, 721-724.
- SIMMONDS, N. W. (1946). Biological flora of the British Isles: *Gentiana pneumonanthe* L. *Journal of Ecology*, **33**, 295-307.
- SMALL, E. (1978). A numerical taxonomic analysis of the *Daucus carota* complex. *Canadian Journal of Botany*, **56**, 248-276.
- SMITH, B. E., MARKS, P. L., & GARDESCU, S. *In press*. Two hundred years of forest cover changes in Tompkins County, New York. *Bulletin of the Torrey Botanical Club*.
- SOUTHWOOD, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337-365.
- SPIRA, T. P. & POLLACK, O. D. (1986). Comparative reproductive biology of alpine biennial and perennial gentians (*Gentiana*: Gentianaceae) in California. *American Journal of Botany*, **73**, 39-47.
- STEARNS, S. C. (1977). The evolution of life history traits: a critique of the theory and a review of the data. *Annual Review of Ecology and Systematics*, **8**, 145-171.
- STONE, W. L. (1840). Rambles in midsummer - Valley of the Genesee, 1840. *Livingston Republican*, December 1.
- STRATTON-PORTER, G. (1925). The Gold Medal Flower. *Tales You Won't Believe*, pp. 75-106. Grossett & Dunlap, New York.
- TESTER, M., SMITH, S. E. & SMITH, F. A. (1987). The phenomenon of "nonmycorrhizal" plants. *Canadian Journal of Botany*, **65**, 419-431.
- THOMPSON, K. (1984). Why biennials are not so few as they ought to be. *American Naturalist*, **123**, 854-861.
- THOREAU, H. D. (1906). *The Writings of Henry David Thoreau: Journals* (Ed by B. Torrey). Houghton Mifflin & Co., Boston.
- TORREY, J. (1843). *A Flora of the State of New York*. Carroll & Cook, Albany.
- TURKINGTON, R. A. & HARPER, J. L. (1979). The growth, distribution and neighbour relations of *T. repens* in a permanent pasture, IV. Fine scale biotic differentiation. *Journal of Ecology*, **67**, 245-254.
- U.S.D.A. (1965). *Soil Survey, Tompkins County, New York*. Soil Conservation Service, U.S.D.A., Government Printing Office, Washington, D.C. Series 1961, No. 25.
- U.S.D.A. (1971). *Soil Survey, Cayuga County, New York*. Soil Conservation Service, U.S.D.A., Government Printing Office, Washington, D.C.
- U.S.D.A. (1973). *Soil Survey, Chemung County, New York*. Soil Conservation Service, U.S.D.A., Government Printing Office, Washington, D.C.
- VAN DER MEIJDEN, E. (1989). Mechanisms in plant population control. *Towards a More Exact Ecology, 30th Symposium of the British Ecological Society* (Ed. by P. J. Grubb & J. B. Whittaker), pp. 163-181. Blackwell, Oxford.

- VAN DER MEIJDEN, E. & VAN DER WAALS-KOOI, R. E. (1979). The population ecology of *Senecio jacobea* in a sand dune system, I. Reproductive strategy and the biennial habit. *Journal of Ecology*, **67**, 131-153.
- VAN DER SLUIS, W. G. & LABADIE, R. P. (1981). Secoiridoids and xanthones in the genus *Centaureum*, Part III: Decentapicrins A, B, and C, New M-hydroxybenzoyl esters of sweroside from *Centaureum littorale*. *Planta Medica*, **41**, 150-160.
- VERKAAR, H. J. & SCHENKEVELD, A. J. (1984a). On the ecology of short-lived forbs in chalk grasslands: life history characteristics. *New Phytologist*, **98**, 659-672.
- VERKAAR, H. J. & SCHENKEVELD, A. J. (1984b). On the ecology of short-lived forbs in chalk grasslands: semelparity and seed output in some species in relation to various levels of nutrient supply. *New Phytologist*, **98**, 673-682.
- VERKAAR, H. J., SCHENKEVELD, A. J. & BRAND, J. M. (1983a). On the ecology of short-lived forbs in chalk grasslands: microsite tolerances in relation to vegetation structure. *Vegetatio*, **52**, 91-102.
- VERKAAR, H. J., SCHENKEVELD, A. J. & VAN DE KLASHORST, M. P. (1983b). The ecology of short-lived forbs in chalk grasslands: dispersal of seeds. *New Phytologist*, **95**, 335-344.
- VERKAAR, H. J. E., VAN DER MEIJDEN, E. & BREEBAART, L. (1986). The responses of *Cynoglossum officinale* L. and *Verbascum thapsus* L. to defoliation in relation to nitrogen supply. *New Phytologist*, **104**, 121-129.
- WARREN, E. R. (1927). *The Beaver - its Work and Ways*. The Williams and Wilkins Company, Baltimore. *Monographs of the American Society of Mammalogists*, **2**.
- WASER, N. M. & PRICE, M. V. (1985). Reciprocal transplant experiments with *Delphinium nelsonii* (Ranunculaceae): evidence for local adaptation. *American Journal of Botany*, **72**, 1726-1732.
- WEBER, H. C. (1984). "Radix Gentianae" (roots of gentians): From extracts of gentian roots to basic research. "Radix Gentianae": vom Enziandestillat zur Grundlagenforschung. *Biologische Rundschau*, **22**, 379-381.
- WELSH, S. L. (1979). Endangered and threatened plants of Utah: a case study. *The Endangered Species: A Symposium*, pp. 69-80. Brigham Young University, Provo, Utah. Great Basin Naturalist Memoirs **3**.
- WERNER, P. A. (1975a). A seed trap for determining patterns of seed deposition in terrestrial plants. *Canadian Journal of Botany*, **53**, 810-813.
- WERNER, P. A. (1975b). Predictions of fate from rosette size in teasel (*Dipsacus fullonum* L.). *Oecologia*, **20**, 197-201.
- WERNER, P. A. (1977). Colonization success of a "biennial" plant species: experimental field studies of species colonization and replacement. *Ecology*, **58**, 840-849.
- WEST, R. G. (1968). *Pleistocene Geology and Biology*. John Wiley and Sons, New York.
- WIEGAND, K. M. & EAMES, A. J. (1926). *The Flora of the Cayuga Lake Basin, New York*. Cornell Agricultural Experiment Station, Ithaca, New York, Memoir **92**.

WINDUS, J. L. (1990). Monitoring *Gentiana saponaria* L. (Gentianaceae); an endangered species in Ohio. *Ecosystem Management: Rare Species and Significant Habitats: Proceedings of the 15th Annual Natural Areas Conference* (Ed by R. S. Mitchell, C. J. Sheviak & D. J. Leopold), pp. 117-118. The State Education Department, Albany, New York. New York State Museum Bulletin No. **471**.

WOOD, C. E. & WEAVER, R. E. (1982). The genera of the Gentianaceae in the southeastern United States: *Sabatia*, *Centaurium*, *Gentiana*, *Gentianella*, *Gentianopsis*, *Frasera*, *Obolaria*, *Bartonia*, *Eustoma*, *Voyria*. *Journal of the Arnold Arboretum*, **63**, 441-487.